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COMPOSITION, MICROGEOGRAPHIC VARIATION, AND SEXUAL DIMORPHISM IN CAATINGAS AND CERRADO BAT COMMUNITIES FROM NORTHEAST BRAZIL

MICHAEL R. WILLIG

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ABSTRACT

Although the South American tropics contains the most diverse chiropteran fauna in the world, most information concerning bats from this region is of a taxonomic or distributional nature. Further, most of our knowledge of Neotropical biology is restricted to locales within mesic predictable biomes. The Brazilian Northeast is an extensive tropical semiarid region characterized by climatic unpredictability and topographic heterogeneity, yet its fauna has never been studied. An 18 month field study of chiropteran populations in Caatingas and Cerrado communities of the Northeast revealed individual, secondary sexual, and microgeographic variation in the bat fauna. Study sites were restricted in size to reduce the probability of sampling bats from different communities while intensive monthly sampling regimes were established to define the faunal composition of each community.

Despite their geographic proximity, the Caatingas and Cerrado contain strikingly different faunas both taxonomically and ecologically. This disparity is most clearly exemplified by the insectivore guilds in each biome. Two hypotheses are proposed to account for the greater diversity of the Caatingas: 1) Large mesic enclaves (serrotes) are common in the Caatingas and probably insulate the fauna from the adverse effects of climatic vicissitudes, whereas great spatial heterogeneity produces distinct habitats for differential exploitation by different bat species, and 2) low insect abundance and diversity on the Chapada as well as reduced canopy complexity within habitats diminishes the number of insectivore niches available within the Cerrado.

Statistical analyses based on 14 external and 16 cranial measurements showed that many species with at least moderate sample sizes display sexual dimorphism, whereas interdemic variation between Caatingas and Cerrado populations is somewhat rarer. The applicability of various hypotheses concerning sexual dimorphism in bats is reviewed in light of the observation that females are larger than males in many bat species. Significant geographic variation between adjacent populations of highly mobile species is maintained in many bat species in the Brazilian Northeast.

INTRODUCTION

The American tropics contains the richest microchiropteran fauna in the world (Patterson and Pascual, 1968). The suborder contains 28.8% of all genera and 27.4% of all species of mammals found in the Neotropics (Walker, 1975). In the more favorable parts of their range, bats may dominate the mammal fauna in terms of both density and species richness (Hershkovitz, 1972). Fifty-two percent of the Costa Rican mammal fauna is composed of bats (Robinson, 1971); similarly, bats represent 46% of the Panamanian mammal fauna (Handley, 1966). In sharp contrast to the situation in the Neotropics, bats represent only 12% of Nearctic mammal species (Walker, 1964). The disparity between northern and southern continents, and the high degree of endemism in the Neotropical bat fauna may be attributed in part to biogeographic conditions. South America, existing as an island from the Cretaceous to late Cenozoic (Dietz and Holden, 1970) would offer great opportunity for chiropteran radiation. The later connection of South America with North America would account in part for the recent occupancy of tropical North America by bats, whereas the subsequent paucity of microchiropteran species might be caused, for the most part, by the vagaries of temperate zone climates.

The taxonomic diversity of Neotropical bats is paralleled by a similar diversity of feeding forms. The year-round abundance of fruits, seeds, nectar, insects and other animals provides sustenance for bats of diverse dietary specializations. Indeed, the adaptive radiation of bats seems to have evolved around the exploitation of many types of food and the partitioning of particular food items by size within general categories (McNab, 1971; Smith and Genoways, 1974). Thus, Neotropical bats occupy a variety of different food niches (frugivory, piscivory, nectarivory, carnivory, insectivory and sanguinivory), whereas Nearctic bats are primarily insectivorous (McNab, 1971; Fleming et al., 1972).

Simpson (1964) was the first to quantify the increase in the number of mammal species as latitude decreases from 60° N latitude to the equator, while MacArthur (1965) attempted to define the factors affecting species diversity to account for the increased richness observed in the tropics. More recently, J. Wilson (1974) has shown that Simpson's original observations are an artifact caused by an exponential increase in the number of bat species with decreasing latitude (see also Mares and Ojeda, 1982). Despite the significant contribution of bats to Neotropical diversity, few works other than the investigations of Flemming et al. (1972), Thomas (1972), and Heithaus et al. (1975) have considered diversity within chiropteran communities. Nonetheless, communities are the context in which species survive and evolve (Whittaker, 1975) and a firm understanding of Neotropical diversity gradients is predicated upon an adequate delineation of the faunal composition of restricted areas within the Neotropics. Many surveys of bat faunas have been made throughout South America, but most have dealt with large geopolitical units (e.g. Husson, 1962; Tuttle, 1970; Handley, 1976; Koopman, 1978). The fauna of broad geographic regions is the sum of the various communities that they contain; however, the differences between communities within a particular biome cannot, in general, be ascertained from such widespread collecting procedures.

Biomes as distinctive as the Caatingas and Cerrado would be expected to harbor unique faunas. Further, due to the unpredictable and severe climatic conditions characteristic of the Caatingas, it would be expected to support a diminished or depauperate fauna when compared to Cerrado habitats. The close proximity of these biomes in the Exu-Crato region of Brazil would effectively eliminate dispersal as a factor affecting the presence or absence of a particular species and thus, climatic or ecological factors should remain as important limiting agents.

Like the previously considered studies of faunal composition, chiropteran systematic studies usually deal with morphometric variation within relatively large areas containing a number of potentially different populations. It is therefore difficult to resolve individual and interdemic variation because samples from particular populations within an area are unidentified or are usually small in size and not amenable to statistical analyses. Further, few comprehensive statistical analyses of chiropteran variation appear in the literature; the works of Taddei (1975a, 1975b, 1979) are an obvious exception for the Phyllostomidae. This study defines and analyzes individual, secondary sexual, and geographic variation of specimens from the Brazilian Northeast. The variation herein reported for bats from both Caatingas and Cerrado populations represents true intrademic variation and the statistical analyses (two-way analysis of variance) permit the isolation of both interdemic and secondary sexual variation, with the subsequent assessment of statistical significance facilitated for each factor.

GENERAL DESCRIPTION OF THE CAATINGAS

The Northeast of Brazil contains five major vegetation zones (see Mares et al., 1981, for a brief description of each zone). Although I was able to make limited surveys in three of these (Atlantic Rainforest, Palm Forest, and Caatinga-Cerrado Contact Zones), the research considered herein is restricted to the Caatingas and Cerrado habitats, where I was able to conduct intensive field work.

The Caatingas (Fig. 1) is an extensive semiarid region lying between 35° and 45° west longitude and 3° and 16° south latitude (Reis, 1976). It occupies approximately 650,000 km^2 (Frota-Pessoa et al., 1971) and is characterized by extreme temporal and spatial climatic variability (Markham, 1972; Markham and McLain, 1977). Annual rainfall may reach 1,600 mm in some areas, yet during drought years other localities may not receive any precipitation at all (Melo, 1956; Markham, 1972). Although cyclic characteristics have been suggested (Markham, 1972, 1974, 1975; and Markham and McLain, 1977), more recent analyses utilizing highly sophisticated statistical techniques indicate that the pattern of rainfall is truly random. As such, the Caatingas has been called the "zone of calamity" (Freise, 1938) and the "region of anomalous drought" (Markham, 1972). Streilein (1981) has succinctly summarized the climatic attributes of the Caatingas. It is sufficient here to note that the variability and distribution of rainfall in the Caatingas is affected by the interrelationships between the Southeast Trade Winds (xeric inducing agents) and three large, mobile, moisture-laden air masses—the equitorial continental mass, the Intertropical Convergence Zone, and the South Atlantic Anticyclone. Precipitation is further affected and diminished by the complex and irregular pattern of orographic barriers (Fig. 2).

Three major geological elements account for the marked topographic relief of the Caatingas (Ab'Saber, 1970). The most extensive component is the basement layer of pre-Cambrian crystalline rock which produces extensive flatlands and gradual slopes. Numerous granitic protrusions in the form

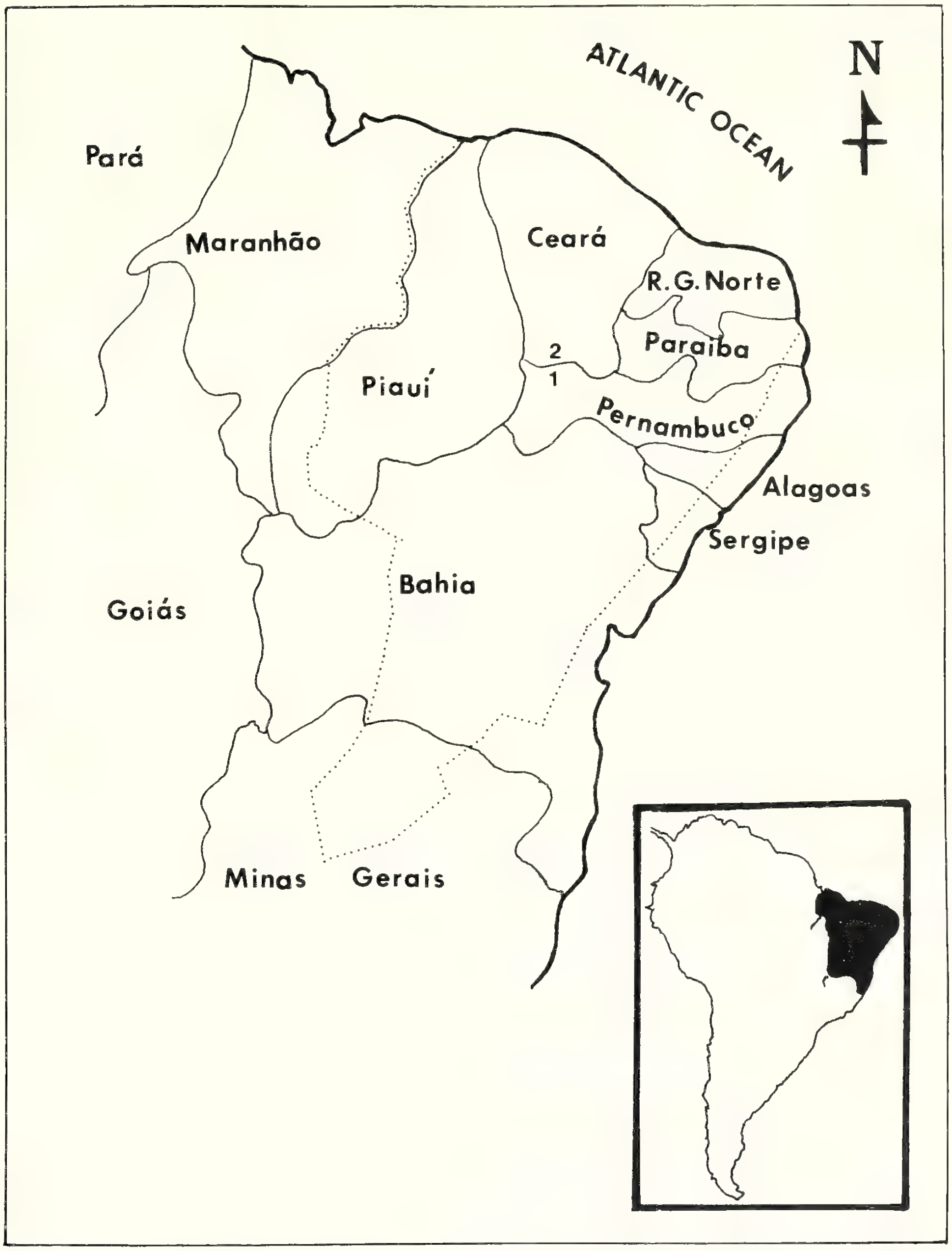

Fig. 1.—The Brazilian Caatingas (delimited by the dotted line) occupies an area of over 650,000 km^2 and is contained within nine states of the Northeast. Because of its irregular shape and susceptibility to extended periods of drought, the region is known as "o poligono das secas" (the polygon of drought). Numbers indicate the location of Caatingas (1) and Cerrado (2) study sites (modified from Mares et al., 1981).

of low mountain ranges (serras), small mountain ridges (serrotes), or lowland outcroppings (lajeiros) punctuate the otherwise flat surface and appreciably increase habitat complexity within the Caatingas. In areas unaffected by post-Cretaceous erosion, the original sandstone substrate still covers the crystalline basement and produces large mesa-like plateaus or chapadas (James, 1942; Ab'Saber, 1970). The elemental composition of these sandstone chapadas, in conjunction with their unique hydrological prop-

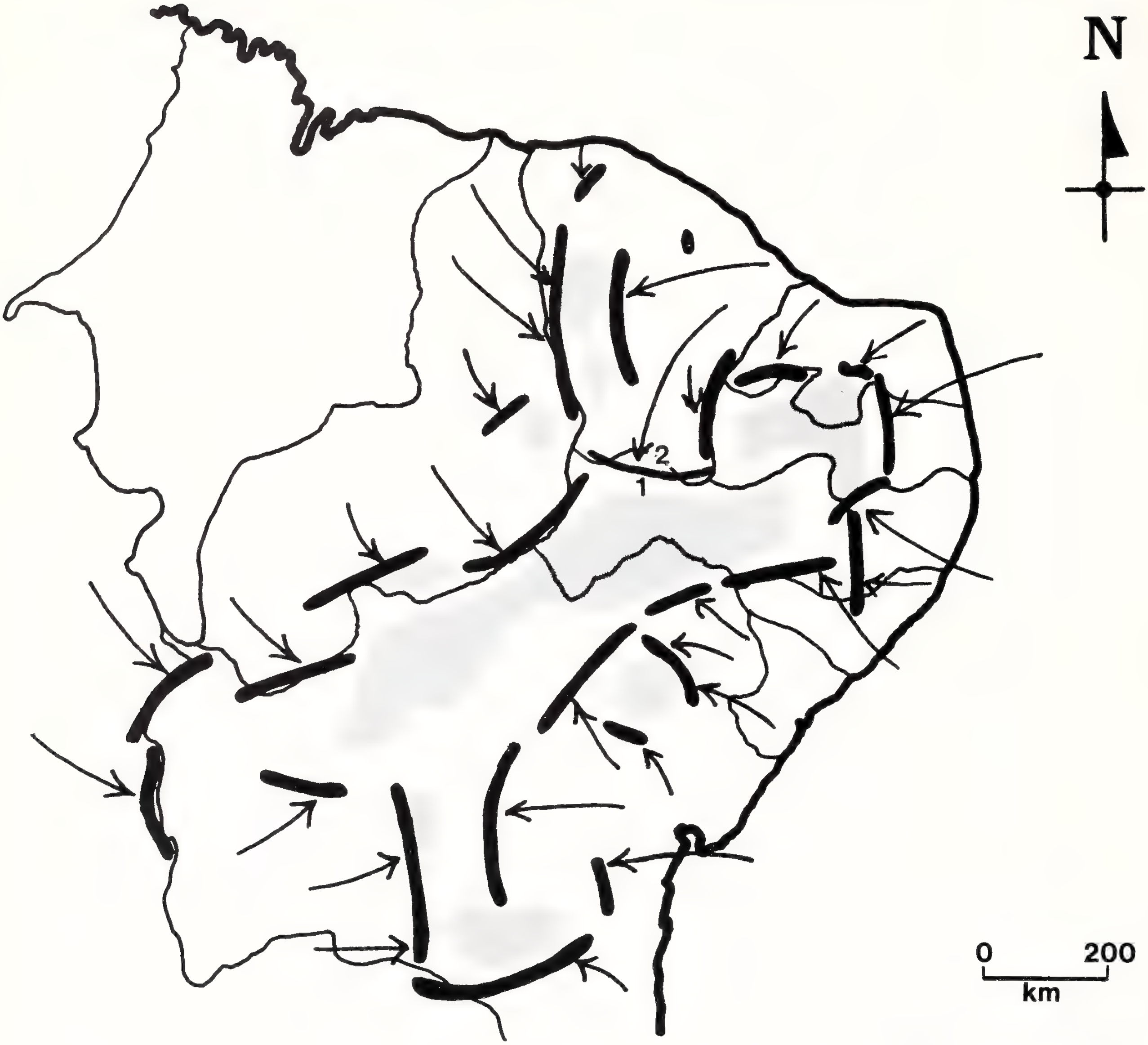

Fig. 2.—The windward side of large chapadas and serrotes (indicated by thick black lines) receive appreciable amounts of orographic rainfall due to the adiabatic cooling of rising air currents (arrows). This produces a rain shadow throughout the interior of the Northeast (shaded area) which is unpredictably subject to periods of severe drought (adapted from Markham, 1972). The Caatingas collection site (1) is located within the rain shadow whereas the Cerrado site (2) is on the windward side of the Chapada do Araripe.

erties, results in extensive edaphic Cerrado habitats occurring in various locations throughout the Northeast.

The zoogeographic affinities of the Caatingas fauna are unclear. Although a prominent biogeographic role has been ascribed to the region (Haffer, 1979; Simpson and Haffer, 1978), Sick (1965), Vanzolini (1974, 1976), Steilein (1981), and Mares et al. (1981) have indicated extremely low levels of vertebrate endemism in both the Caatingas and interdigitating Cerrado habitats.

In general, the mammal faunas of the Caatingas and Cerrado appear to be quite similar (Guimaraes, 1972), with elements from the Amazon Basin, Atlantic Rainforest and the Chaco xeric belt composing the major portion of each fauna. An analysis of

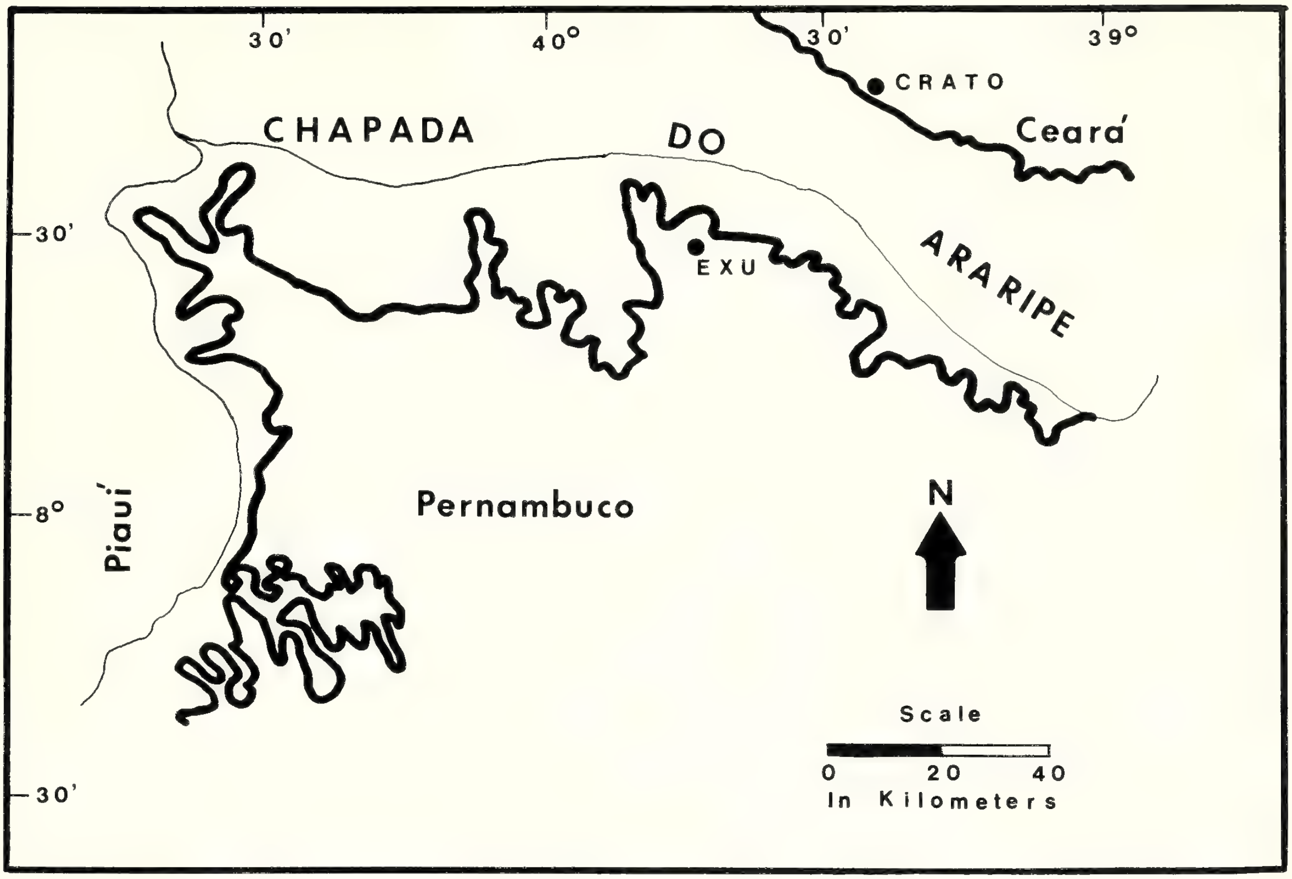

Fig. 3.—The Chapada do Araripe, a large sandstone plateau, dominates the landscape in the vicinity of both the Caatingas (Exu, Pernambuco) and Cerrado (Crato, Ceará) study sites. Caatingas study sites are located at least 10 to 15 km from the base of the Chapada. The Cerrado study area is located in the Floresta Nacional Araripe-Apodí on the top of the Chapada do Araripe, south of the city of Crato, Ceará. Heavy lines indicate the edge of the Chapada while thin lines indicate state boundaries (modified from Dias, 1960).

the non-volant mammal distribution patterns and a re-analysis of other vertebrate groups from the Caatingas (Mares et al., unpublished manuscript) indicates that the Caatingas was not an effective xeric refugium for mammals during more mesic times of the Pleistocene. Like the rainfall patterns that characterize the area, the Caatingas small-mammal fauna is anomalous, lacking the obvious physiological and morphological adaptations expected in a xeric environment.

STUDY SITES

My research was primarily restricted to the geographic center of the Caatingas in order to take advantage of the complete array of habitats available. Field work was equally divided between the municipality of Exu, Pernambuco, and the adjacent municipality of Crato, Ceará, in the Floresta Nacional Araripe-Apodí. The area is extremely complex; all three major geological formations characteristic of the Northeast are in close proximity with both Caatingas and Cerrado habitats represented. An extensive plateau, the Chapada do Araripe, dominates the landscape and extends for many miles along the border between Ceará and Pernambuco (Fig. 3). The Chapada has a pronounced effect on

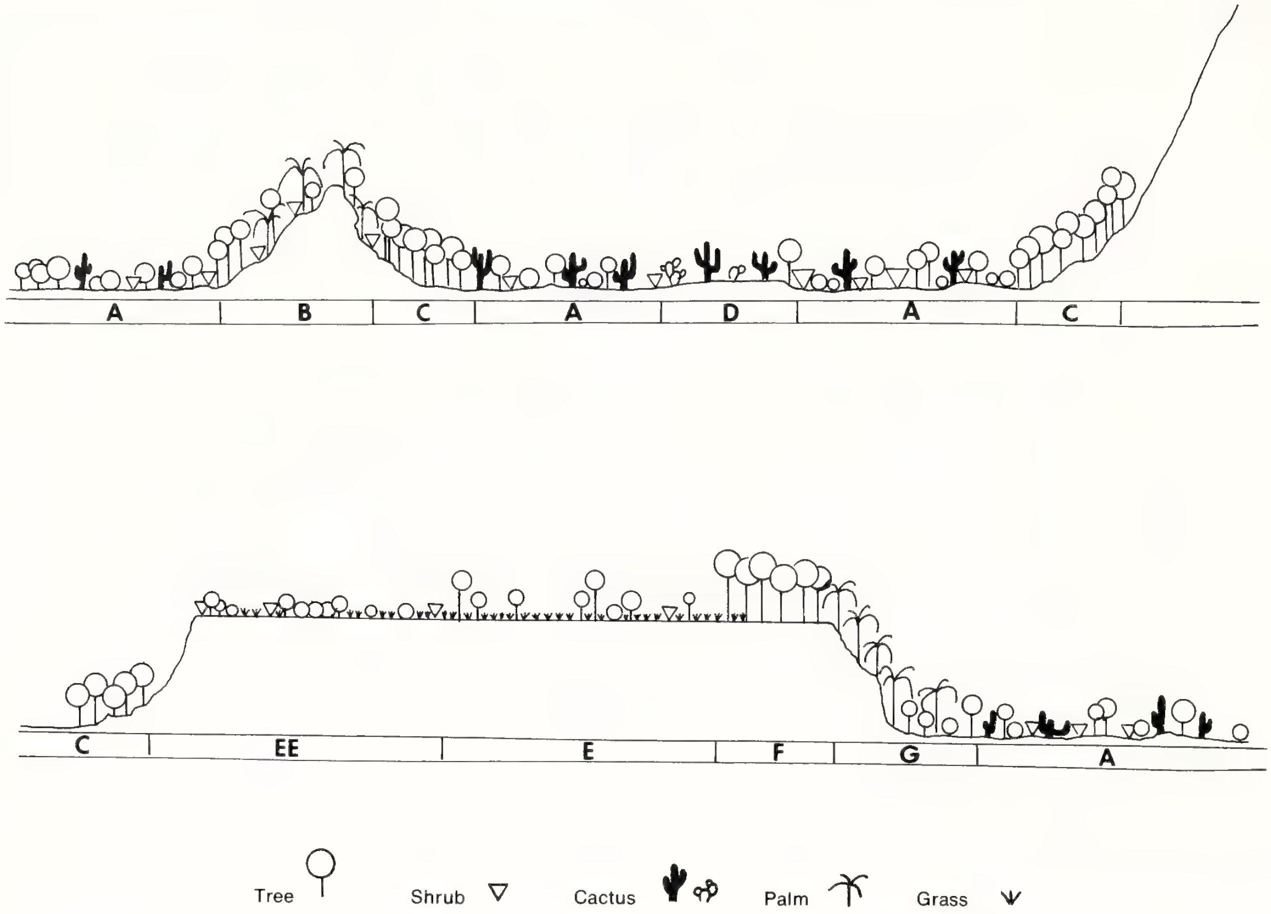

Fig. 4.—Schematic representation of the mosaic of habitats in the Caatingas and their proximity to Cerrado vegetation on the Chapada do Araripe and to humid forest in areas of orographic rainfall. Key to habitat types: A) Caatinga Baixa; B) Serrote; C) Caatinga Alta; D) Lajeiro; E) Cerrado; EE) disturbed areas; F) Cerradão; G) humid forest.

local rainfall patterns. On its windward side (Crato, Ceará), orographic precipitation produces conditions more conducive to mesic tropical vegetation, whereas on its leeward side (Exu, Pernambuco), xeric Caatingas vegetation predominates. The sandstone composition of the Chapada, in conjunction with elevated precipitation and lowered temperatures supports an edaphic form of Cerrado vegetation within the confines of the Caatingas proper. A schematic representation of the mosaic of habitats present in the Caatingas and their relationship to the Chapada do Araripe and Cerrado habitats is illustrated in Fig. 4.

THE CAATINGAS

In general, the Caatingas contains a variable assemblage of xeric-adapted plants. Much of the flora is characteristically deciduous during periods of water deficit, but members of the Cactaceae and Euphorbiaceae conspicuously exploit an alternate strategy of reduced leaf area and increased water storage capacity. The substantial xerophytic adaptations of the Caatingas flora, especially those exhibited by the Cactaceae and Euphorbiaceae demonstrate that this region has been subjected to xeric conditions for a substantial period of time (Alvim, 1949). Based upon vegetational physiognomy and local geology, four different Caatingas habitats may be distinguished—Caatinga Baixa (Low Caatinga), Caatinga Alta (High Caatinga), Serrotes, and Lajeiros (Fig. 5). Floral composition is often variable both within and between habitats; thus it is not the most effective criterion for defining habitat types.

Caatinga Baixa

Throughout lower elevations in the Exu region, Caatinga Baixa habitat predominates (Fig. 6). This is the most extensive habitat found in the region

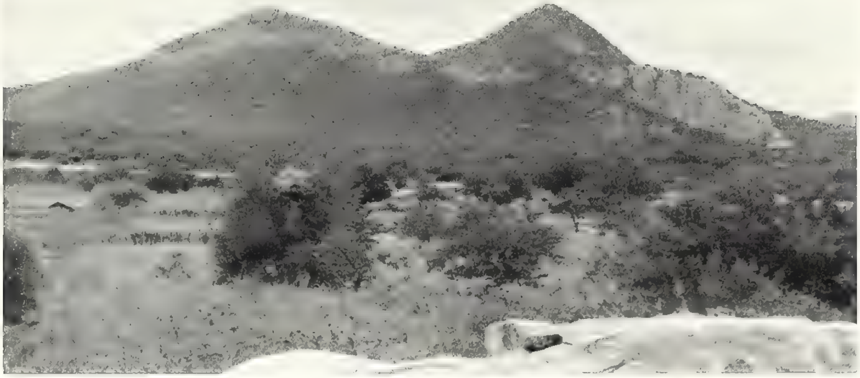

Fig. 5.—Panoramic view of Caatingas habitats illustrating serrotes (in the background) with Caatinga Alta vegetation present on the slopes. The foreground contains fields in various stages of ecological succession.

because it is associated with the ubiquitous non-granitic crystalline substrata in the Northeast. Plant species composition differs greatly between localities; however, the vegetation is quite dense and many of the most common plants are shared between sites (see Mares et al., 1981). Trees are xerophytic and may reach a height of 3 to 5 m while occasional emergents may attain a height of 8 m. Large cacti such as *Cereus jamacaru* (Mandacaru), *Cephalocereus gounellei* (Xique-xique), and *Zehntherella squamulosa* (Facheiro) are common components, especially visible during dry periods. Minor differences in topography, variation in soil parameters, prior utilization by man, and differential exploita-

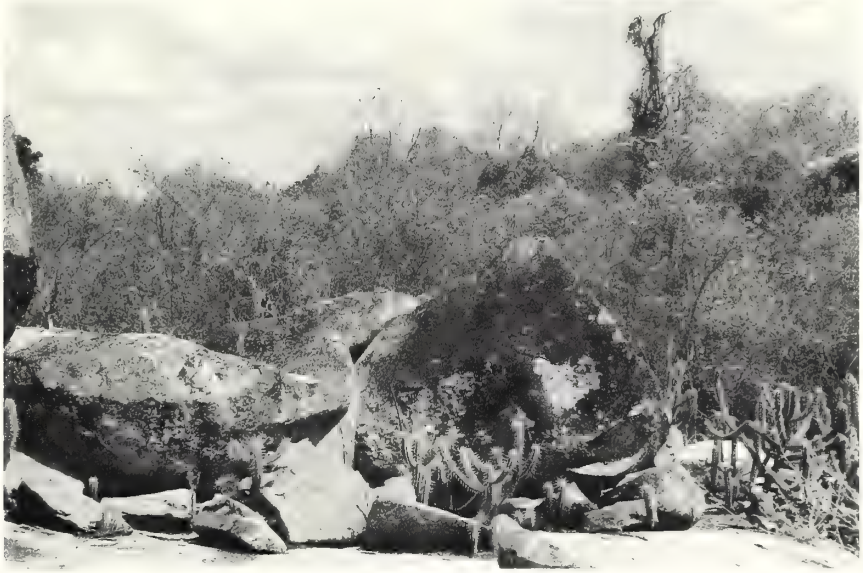

Fig. 6.—A locality in Exu, Pernambuco, containing a Lajeiro in the foreground with typical Caatinga Baixa vegetation in the background.

tion by domestic animals generate microhabitat mosaics which defy categorization using only a few broad generalizations.

Caatinga Alta

Larger xerophytic trees (10–12 m) characterize Caatinga Alta (see Mares et al., 1981). They typically lose their leaves in synchrony during the dry season and form a closed canopy in the wet season. The understory is poorly developed and density is lower than in Caatinga Baixa habitats. Caatinga Alta habitats are restricted to higher elevations, hillsides, and the perimeters of gentle valleys formed by serrotes and serras; these habitats are, therefore, more mesic than the surrounding Low Caatinga sites (Fig. 5). Small rock outcroppings or rock piles are dispersed throughout the forest floor, but rarely reach sizes greater than 25 m^2.

Lajeiros

Lajeiros are granitic rock outcroppings, principally distributed throughout areas dominated by Caatinga Baixa (Fig. 6). They are variable in both size and shape although they usually do not exceed a height of 15 m. In their simplest form, lajeiros may be small unbroken rock faces but at the other extreme, their area would best be measured in hectares. These expansive formations may be composed of rock faces containing many fissures studded with cacti and strewn with boulders of variable size and shape. *Pilosocereus gounelli, Cereus jamacaru,* and *Opuntia palmadora* (Palma) are the cacti most frequently associated with these outcroppings. Complex lajeiros appreciably magnify topographic complexity in the Caatingas (Mares et al., 1981); they appear to offer mesic refugia for many species of non-volant mammals (Lacher, 1981; Streilein, 1981) and thus are important habitats influencing mammal distribution patterns.

Serrotes

Numerous granitic serrotes are found in the municipality of Exu (see Figs. 3, 4 and 5). These mountain ridges harbor the most mesic components of the Caatingas flora and remain green for extended periods during the dry season. These areas, termed "brejos" by Andrade and Lins (1964), contain floral affinities with the Atlantic Rainforest vegetation and are important mesic refugia for both plants and animals in the Caatingas. Localities of increased orographic rainfall, like serrotes, are common throughout the Caatingas; the state of Pernambuco alone contains 22 major brejos (Andrade and Lins, 1964). Palms such as *Syargus oleracea* and *Accrocomia intumescens* are typically restricted to serrotes having increased orographic rainfall. Because the upper limits of Caatinga Alta also occur on the slopes of serrotes, there are places where substantial intermingling of their constituent vegetation occurs.

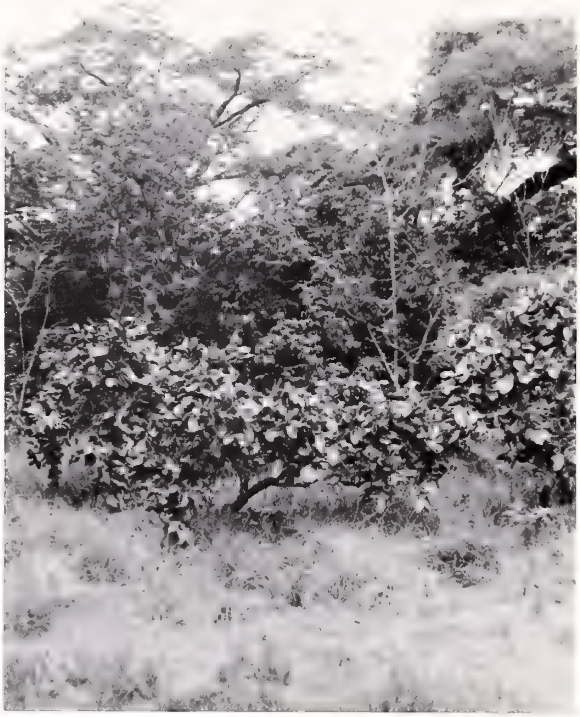

Fig. 7.—A typical locality on the Chapada do Araripe (Crato, Ceará) exhibiting three of the characteristic components of Cerrado habitats—pervasive grass species, small shrubs, and gnarled trees.

THE CHAPADA DO ARARIPE

The Floresta Nacional Araripe-Apodí contains most of the collection sites examined on the Chapada do Araripe. The plateau is characterized by a thin layer of sandy red soil covering a hard sandstone substrate. Rocks, boulders, and stones are absent from the Chapada as are permanent bodies of water. During the rainy season, low lying depressions may be covered with temporary pools con-

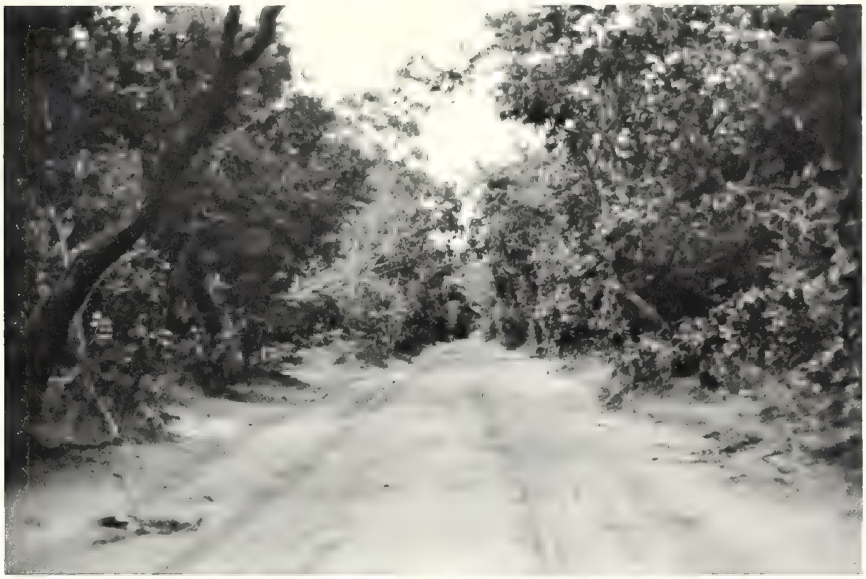

Fig. 8.—A road cutting through Cerradão vegetation at the edge of the Chapada do Araripe (Crato, Ceará). Large trees and a closed canopy distinguish this habitat from Cerrado.

taining from 6 to 12 inches of water. In general, the vegetation is sclerophyllous and semideciduous. Trees and shrubs lose their leaves each year, but leaf loss is asynchronous both intra- and interspecifically. Based upon physiognomy and density, two kinds of habitats are recognizable on the Chapada—Cerrado and Cerradão. Their relationship to each other and Caatingas vegetation is shown in Fig. 4.

Cerrado

Physiognomically, the Cerrado on the Chapada do Araripe is an open tree and shrub woodland with a pervasive grass component (Fig. 7). Small trees (3–5 m) and shrubs (0.5–3 m) form approximately half of the vegetation cover, and various grass species occupy the remaining area. Taller trees, rarely exceeding a height of 15 m are scattered throughout the area. As a result, the canopy is open, irregular and undulating in profile, with numerous areas lacking woody plants. The taller trees and shrubs have characteristically gnarled trunks and twisted branches; root penetration into the sandstone bedrock is minimal. The most common trees, shrubs, and grasses are listed in Mares et al. (1981).

Cerradão

Sections of the Floresta Nacional Araripe-Apodí, for the most part bordering the windward side of the Chapada do Araripe, differ substantially from Cerrado vegetation in plant density, physiognomy, and species importance. Stands with very little grass, few shrubs, and numerous trees are herein referred to as Cerradão (Fig. 8). Larger trees compose Cerradão habitats and form a closed canopy between 12 and 17 m high. These trees do not have the gnarled appearance characteristic of the Cerrado. The understory may vary from quite dense to sparse; however, in either situation, small shrubs (~1 m) and grasses are rare.

MATERIALS AND METHODS

Faunal Composition

Bats were collected by netting from September 1976 to May 1978 in Caatingas (Municipality of Exu, Pernambuco) and Cerrado (Chapada do Araripe, Municipality of Crato, Ceará) habitats in northeastern Brazil. I was interested in determining the composition of one community within the Caatingas and another within the Cerrado, so only monthly samples from within a restricted area were utilized in subsequent analyses. Sampling locales were contained within a circular area whose radius was 10 km in both biomes, and five to ten locales within that area were

Table 1.—*Description of external and cranial characters measured on specimens of bats captured in Exu, Pernambuco (Caatingas), and Crato, Ceará (Cerrado).*

External Characters

Total length: greatest distance from the anteriormost portion of the snout to the distal point of the tail.

Tail length: greatest distance from the distal caudal vertebra to the angle made by the tail when positioned perpendicular to the body.

Hind foot length: distance from the heel of the foot to the tip of the longest toe including the claw.

Ear length: distance from the basal notch of the ear to the furthermost point on the edge of the pinna.

Tragus length: distance from the base of the tragus to its distal edge.

Forearm length: distance from the outside of the wrist to the outside of the elbow when the wing is folded.

Weight: weight of the fresh specimen.

Length of digit one: length from the wrist to the distalmost point of the first digit, including the claw.

Length of digit three: length from the wrist to the distal point on the phalange of digit three when the wing is maximally extended.

Length of digit four: length from the wrist to the distal point on the phalange of digit four when the wing is maximally extended.

Length of digit five: length from the wrist to the distal point on the phalange of digit five when the wing is maximally extended.

Tibia length: length from the outermost point of the ankle to the outermost point of the knee.

Calcar length: length from the distal point of the calcar to the angle made by the calcar when it is positioned perpendicular to the leg.

Noseleaf length: length from the distalmost point of the noseleaf to its juncture with the rostrum.

Cranial Characters

Greatest length of skull: distance from the most anterior part of the rostrum (excluding teeth) to the posteriormost point of the skull.

Condylobasal length: distance from the anteriormost edge of the premaxillae to the posteriormost projection of the occipital condyles.

Zygomatic breadth: greatest distance between the outer margins of the zygomatic arches.

Postorbital constriction: least distance across the top of the skull posterior to the postorbital process.

Mastoid breadth: greatest width of the skull, including the mastoid.

Breadth of the braincase: greatest width across the braincase posterior to the zygomatic arches.

Rostral breadth: width of the rostrum at the suture between premaxillae and maxillae.

Height of the braincase: greatest height of the braincase from a line perpendicular to the long axis of the skull (+1 mm).

Breadth across the upper molars: maximum width from the outer alveolus of one molar to the outer alveolus of another.

Breadth across the upper canines: width from the outer alveolus of one canine to the outer alveolus of the other canine.

Length of maxillary tooth row: length from the anterior edge of the alveolus of the first tooth present in the maxillae to the posterior edge of the alveolus of the last molar.

Table 1.—*Continued.*

Length of the upper molariform toothrow: maximum length from the anterior edge of the alveolus of the first cheek tooth to the posterior edge of the alveolus of the last molar.

Width of widest molar: width of widest molar in the maxilla exlcuding the alveolus.

Greatest length of the mandible: length from the anteriormost point on the ramus (excluding teeth) to the posteriormost point on the coronoid process.

Length of mandibular tooth row: length from the anterior edge of the alveolus of the canine to the posterior edge of the alveolus of the last molar in the mandible.

Length of coronoid process: distance from the posteriormost point on the coronoid process to the base of the ramus.

visited each month. Standard Japanese mist nets (10 m by 2 m) were used to collect specimens. Although the position of the nets was determined by peculiarities of the terrain and the physiognomy of the vegetation, I was usually able to erect 10 sections of netting per night in the most frequented collection sites. All nets were positioned before dusk and checked at 15-min intervals or sooner depending upon the level of bat activity. Because activity usually was quite high at most collection sites, the nets were, in effect, monitored continuously. Nets remained open for a minimum of 3.5 to 4 h each night. Initial field work indicated that additional netting was counter-productive; total activity diminished drastically after 2100–2130 hours and the same species caught earlier in the night were caught during later time periods. Supplemental collecting from roosts (for example, caves, tree hollows, buildings, culverts, etc.) was also done in order to verify that the faunal composition was not biased by collecting techniques. Half of the collection is housed in the Carnegie Museum of Natural History; the other half is deposited in the Museu de Zoologia da Universidade de São Paulo in Brazil.

INDIVIDUAL, SECONDARY SEXUAL, AND GEOGRAPHIC VARIATION

When collections were sufficiently large, 14 external characteristics and 16 cranial characteristics were determined for a sample of 20 adult males and 20 adult females from both Caatingas and Cerrado habitats. Otherwise the entire collection from each biome was used in subsequent analyses. Table 1 lists and describes all of the characters used throughout the statistical analyses. External characters were measured to the nearest millimeter utilizing a metric ruler; cranial characters were measured with metric dial calipers to the nearest hundredth of a millimeter.

Individual variation was determined for males and females within both Caatingas and Cerrado communities. The standard deviation (SD) and coefficient of variation were utilized as statistical estimates of individual variation for each mensural character.

Two-way analysis of variance was utilized to ascertain the existence of geographic and secondary sexual variation in species with sufficiently large samples of males and females from both Caatingas and Cerrado biomes. When samples were small for one or both biomes, the data were combined and secondary sexual variation was examined utilizing one-way analysis of variance; this technique also was utilized for species found only in one biome. Levene's test for homogeneity of variance was performed on all variables in order to determine the appropriateness of the analysis of variance.

Sexual dimorphism for *size* is indicated when a particular sex consistently has larger sample means than the opposite sex and many of those characters exhibit statistically significant sexual variation. If the actual differences between population mean values is small, large samples are required to detect statistical significance between sample means; in such cases where samples are small the consistent observation of larger mean values for a particular sex suggests sexual dimorphism for size but is inconclusive until larger samples can be obtained. Sexual dimorphism for shape occurs when many characters exhibit statistically significant secondary sexual variation but obvious trends for mean value relations do not exist.

RESULTS AND DISCUSSION

Faunal Composition

Over 5,000 bat specimens representing 38 species, 29 genera, and eight families were captured during this study; 65% of the mammalian species known from the Exu-Crato area are members of the Chiroptera. Table 2 lists the bat species from this study in systematic order, indicates their relative abundance in Caatingas or Cerrado biomes, and identifies their feeding guild associations. Twenty species are shared between biomes; further, the Caatingas contains 13 species not found in the Cerrado, whereas the Cerrado contains five species not found in the Caatingas. If only the non-rare species in each biome are considered, the dissimilarities between areas become more pronounced—15 of the 24 species (over half of the species pool) occur exclusively in one or the other of the areas. Despite their geographic proximity, the Caatingas and Cerrado habitats contain markedly different bat faunas.

Contrary to my earlier prediction, the Caatingas community is more species rich than the Cerrado community. A more detailed examination of the distribution of bats within each community suggests an explanation for this observation. Faunal composition and species densities are rather uniform throughout Cerrado habitats on the Chapada do Araripe. Conversely, the Caatingas is quite heterogeneous in this regard. Caatinga Baixa contains few species of bats, and those species present occur at low densities. Lajeiros contain a few additional species (*Neoplatymops mattogrossensis* and *Peropteryx macrotis*), but in general, the fauna of the Caatingas in low-lying areas (Caatinga Baixa and lajeiros) is depauperate. Species of foliage gleaning insectivore (*Mimon crenulatum, Micronycteris megalotis, Micronycteris minuta,* and *Tonatia brasiliense*) reach their highest density and occur almost exclusively in Caatinga Alta. With few exceptions, however, serrotes harbor the bulk of the species found in the Caatingas and it is on serrotes or the adjacent areas of Caatinga Alta that most species reach their highest densities. Thus, the relatively high species richness of the Caatingas can be attributed in part to the topographic relief and vegetational diversity of the Caatingas, but equally important from the point of view of the Chiroptera, the numerous serrotes punctuating the flat landscape of the Caatingas provide roosting sites and mesic refugia during drought periods.

Frugivore guilds in the Caatingas and Cerrado are quite similar in terms of species richness and taxonomic composition. The main distinction among the guilds is the greater density of all frugivorous species on the Chapada and the presence there of an additional small species, *A. concolor.* The presence of *L. mordax* in the Caatingas is the most obvious difference between the biomes with respect to nectarivores. Neither frugivores nor nectarivores appreciably affect the faunal differences between the Caatingas and Cerrado.

The notable absence of sanguinivores and piscivores from among the common Cerrado bats diminishes the diversity of that fauna. Large native mammals are absent from the Chapada and domestic species are prohibited by law from entering the Floresta Nacional Araripe-Apodí. Thus, it is not surprising to find vampires rare in Chapada habitats. The absence of standing bodies of water from the Chapada accounts for the rareness of piscivores.

The disparity between the Caatingas and Cerrado bat faunas is most clearly manifested within the various insectivore guilds. The Caatingas harbors a diverse insectivore fauna; five species of foliage gleaning insectivores, two species of aerial insectivores, and two species of molossid insectivores reach appreciable densities there. In contrast, *M. nigricans, E. furinalis,* and *M. molossus* are the only insectivorous bats that attain appreciable densities

Table 2.—*Systematic listing of bats from Caatingas (Exu, Pernambuco) and Cerrado (Crato, Ceará) biomes; A indicates abundant, C indicates common, R indicates rare, and—indicates absent. Feeding guild abbreviations: AERIN, aerial insectivore; PISCI, piscivore; FOLGL, foliage-gleaning insectivore; OMNIV, omnivore; NECTA, nectarivore; FRUGI, frugivore; SANGU, sanguinivore; MOLOS, molossid aerial insectivore.*

	Species	Presence		Guild
		Caatingas	Cerrado	
Family	Emballonuridae			
	Saccopteryx leptura	—	R	AERIN
	Peropteryx macrotis	C	—	AERIN
Family	Noctilionidae			
	Noctilio leporinus	C	R	PISCI
Family	Mormoopidae			
	Pteronotus davyi	R	R	AERIN
Family	Phyllostomidae			
Subfamily	Phyllostominae			
	Micronycteris megalotis	R-C	R	FOLGL
	Micronycteris minuta	R-C	R	FOLGL
	Tonatia bidens	R	—	FOLGL
	Tonatia brasiliense	R-C	—	FOLGL
	Tonatia silvicola	C	—	FOLGL
	Milmon crenulatum	R-C	—	FOLGL
	Phyllostomus discolor	R-C	A	OMNIV
	Phyllostomus hastatus	R	A	OMNIV
	Trachops cirrhosus	C	—	OMNIV
Subfamily	Glossophaginae			
	Glossophaga soricina	A	A	NECTA
	Lonchophylla mordax	C	—	NECTA
	Anoura geoffroyi	R	C	NECTA
Subfamily	Carolliinae			
	Carollia perspicillata	A	A	FRUGI
Subfamily	Stenodermatinae			
	Sturnira lilium	R	C-R	FRUGI
	Uroderma magnirostrum	R	R	FRUGI
	Vampyrops lineatus	A	A	FRUGI
	Artibeus concolor	—	C-R	FRUGI
	Artibeus jamaicensis	C	A	FRUGI
	Artibeus lituratus	C-R	A	FRUGI
Subfamily	Desmodontinae			
	Desmodus rotundus	A	R	SANGU
	Diphylla ecaudata	R	—	SANGU
Family	Natalidae			
	Natalus stramineus	—	R	AERIN
Family	Furipteridae			
	Furipterus horrens	R	—	AERIN
Family	Vespertilionidae			
	Myotis nigricans	C-A	C	AERIN
	Eptesicus furinalis	—	C-R	AERIN
	Lasiurus borealis	—	R	AERIN
	Lasiurus ega	R	R	AERIN
Family	Molossidae			
	Molossops planirostris	R	—	MOLOS
	Molossops temminckii	R	R	MOLOS
	Tadarida laticaudata	R	R	MOLOS
	Neoplatymops mattogrossensis	C	—	MOLOS
	Molossus ater	R	—	MOLOS
	Molossus molossus	A	A	MOLOS
	Eumops sp.	R	—	MOLOS

on the Chapada do Araripe, and their presence is primarily restricted to disturbed areas containing abandoned buildings. None of the common Cerrado insectivores glean their prey from foliage. The savanna-like characteristics of the Chapada (that is, open spaces, low canopy, reduced vertical stratification within the canopy) as well as the depauperate nature of the Cerrado insect fauna limit the potential number of insectivore niches available for bats to exploit and to a large extent accounts for the depauperate nature of the Cerrado bat fauna in general.

SPECIES ACCOUNTS

Family Emballonuridae

Saccopteryx leptura Schreber, 1774

This aerial insectivore was absent from the Caatingas and was quite rare on the Chapada do Araripe. Further, the specific designation of *S. bilineata* was applied to both specimens of *S. leptura* from the Chapada do Araripe by Mares et al. (1981). Very little is known about the biology of *S. leptura* and only isolated records of mensural characters appear in the literature. Statistical analyses could not be performed on the sample of two individuals obtained from the Chapada do Araripe; hence only selected individual measurements (after Swanepoel and Genoways, 1979) are reported here for an adult female and an adult male (total length, 61, 69; tail length, 17, 14; hindfoot length, 6, 6; ear length, 13, 13; greatest length of skull,—, 13.3; condylobasal length, —, 121; zygomatic breadth, —, —; postorbital constriction, 2.3, 2.3; breadth of braincase, 6.8, 6.9; length of the maxillary toothrow, 5.4, —; breadth across the upper molars, 6.2, —).

Peropteryx macrotis (Wagner, 1843)

Of the three subspecies presently recognized, only *P. m. macrotis* occurs on the mainland of South America (Cabrera, 1957). Although uncommon in the Caatingas, this aerial insectivore was found roosting in small aggregations of up to 10 individuals in large openings inside rockpiles or culverts. Over a 6 month period, the number of individuals in each of two monitored roosting sites remained constant. Further, each roost contained only one adult male. This suggests that *P. m. macrotis* males might maintain small harems and exhibit resource defense polygony when appropriate roosting conditions are available. Distances between neighboring individuals in the roost varied from 15 to 60 cm. Individuals roosted by anchoring their feet and thumbs to the ceiling of the retreat site; hence, their bodies assumed an acute angle with respect to the overlying rock stratum. These bats were frequently observed leaving their roosts before dusk. The absence of *P. m. macrotis* from the Chapada do Araripe can most easily be explained by the lack of suitable roosting sites.

The results of the statistical analyses of 13 external and 16 cranial characters on specimens from the Chapada do Araripe are summarized in Table 3. Sample means for females are larger than sample means for males for 10 external characters and 15 cranial characters; statistically significant differences exist for total length, tragus length, forearm length, length of digit III, length of digit V, condylobasal length, breadth across the upper molars, breadth across the upper canines, and greatest length of the maxillary. The sample means for males are larger than those for females for three external and one cranial character; none exhibit statistically significant differences. Sexual dimorphism with females larger than males is clearly supported by the data.

Family Noctilionidae

Noctilio leporinus (Linnaeus, 1758)

Of the three subspecies of this piscivore currently recognized, *Noctilio l. leporinus* is the appropriate designation for specimens from the Northeast of Brazil (Davis, 1973). It was exceptionally rare on the Chapada do Araripe; the few individuals caught there were probably transients from surrounding habitats. It was common in the Caatingas where it roosted during the day in groups of up to 30 individuals. The large hollow hardwood trees typically found in Caatinga Alta habitats provided its preferred diurnal roosting sites. Sex ratios did not significantly differ from one to one based upon overall netting records or data from individual day roosts (Binomial Test, $P > .05$). Approximately 47% of the 328 captured adult specimens from the Caatingas were males.

Individuals frequently foraged at small lakes and ponds in groups containing five to 15 bats. Individuals seemed to coordinate feeding activities and concentrated foraging activity on the periphery of bodies of water. A concrete bridge which traversed a semipermanent stream contained a nocturnal feeding roost that was used by over 150 individuals. This roost was in continual use for the duration of

Table 3.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, N) of* Peropteryx macrotis *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	61.33	64.14			Sex	1	37.673	5.30	.032
SD	1.99	3.81			Within	20	7.110		
SE	.51	1.44							
CV	3.24	5.94							
n	15	7							
Tail length									
Mean	14.20	14.14			Sex	1	.016	.00	.945
SD	1.61	2.12			Within	20	3.163		
SE	.42	.80							
CV	11.34	14.99							
n	15	7							
Hindfoot length									
Mean	6.60	6.57			Sex	1	.004	.01	.919
SD	.51	.79			Within	20	.366		
SE	.13	.30							
CV	7.73	12.02							
n	15	7							
Ear length									
Mean	14.20	14.43			Sex	1	.249	.49	.491
SD	.56	.98			Within	20	.506		
SE	.15	.37							
CV	3.94	6.79							
n	15	7							
Tragus length									
Mean	6.13	6.71			Sex	1	1.611	6.25	.021
SD	.52	.49			Within	20	.258		
SE	.13	.18							
CV	8.48	7.30							
n	15	7							
Forearm length									
Mean	42.00	43.57			Sex	1	11.786	13.31	.002
SD	.85	1.13			Within	20	.886		
SE	.22	.43							
CV	2.02	2.59							
n	15	7							
Weight									
Mean	4.23	4.57			Sex	1	.546	1.08	.312
SD	.59	.93			Within	20	.507		
SE	.15	.35							
CV	13.95	20.35							
n	15	7							
Length of digit one									
Mean	7.53	7.14			Sex	1	.728	1.00	.330
SD	.74	1.07			Within	20	.730		
SE	.19	.40							
CV	9.83	14.99							
n	15	7							

Table 3.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Length of digit three				
Mean	64.67	68.00			Sex	1	53.03	5.91	.025
SD	2.38	4.08			Within	20	8.97		
SE	62	1.54							
CV	3.68	6.00							
n	15	7							
					Length of digit four				
Mean	45.80	47.43			Sex	1	12.658	3.01	.098
SD	1.37	3.10			Within	20	4.206		
SE	.36	1.17							
CV	2.99	6.54							
n	15	7							
					Length of digit five				
Mean	44.40	46.86			Sex	1	28.82	12.41	.002
SD	1.35	1.86			Within	20	2.32		
SE	.35	.71							
CV	3.04	3.97							
n	15	7							
					Tibia length				
Mean	18.80	19.14			Sex	1	.561	1.21	.284
SD	.56	.90			Within	20	.463		
SE	.15	.34							
CV	2.98	4.70							
n	15	7							
					Calcar length				
Mean	15.80	16.14			Sex	1	.561	.34	.568
SD	1.27	1.35			Within	20	1.660		
SE	.33	.51							
CV	8.04	8.36							
n	15	7							
					Greatest length of skull				
Mean	13.75	13.99			Sex	1	.258	3.67	.070
SD	.30	.17			Within	20	.070		
SE	.08	.06							
CV	2.18	1.22							
n	15	7							
					Condylobasal length				
Mean	12.74	13.03			Sex	1	.397	5.00	.037
SD	.25	.35			Within	20	.080		
SE	.06	.13							
CV	1.96	2.69							
n	15	7							
					Zygomatic breadth				
Mean	8.15	8.31			Sex	1	.134	3.91	.480
SD	.16	.23			Within	20	.034		
SE	.04	.09							
CV	1.96	2.77							
n	15	7							

Table 3.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	2.47	2.50			Sex	1	.003	.15	.702
SD	.15	.14			Within	20	.023		
SE	.04	.05							
CV	6.07	5.60							
n	15	7							
Mastoid breadth									
Mean	7.25	7.27			Sex	1	.003	.08	.786
SD	.13	.30			Within	20	.039		
SE	.03	.12							
CV	1.79	4.13							
n	15	7							
Breadth of braincase									
Mean	6.49	6.49			Sex	1	.000	.00	.989
SD	.16	.09			Within	20	.020		
SE	.04	.03							
CV	2.47	1.39							
n	15	7							
Rostral breadth									
Mean	5.97	6.15			Sex	1	.134	2.45	.135
SD	.23	.24			Within	18	.055		
SE	.06	.10							
CV	3.85	3.90							
n	14	6							
Height of braincase									
Mean	7.45	7.50			Sex	1	.009	.16	.692
SD	.26	.18			Within	19	.058		
SE	.07	.07							
CV	3.49	2.40							
n	15	6							
Breadth across the upper molars									
Mean	6.02	6.48			Sex	1	.896	13.53	.002
SD	.21	.35			Within	18	.066		
SE	.06	.14							
CV	3.49	5.40							
n	14	6							
Breadth across the upper canines									
Mean	3.47	3.67			Sex	1	.160	6.52	.020
SD	.14	.19			Within	18	.025		
SE	.04	.08							
CV	4.03	5.18							
n	14	6							
Length of the maxillary toothrow									
Mean	5.49	5.53			Sex	1	.007	.16	.695
SD	.18	.27			Within	19	.043		
SE	.05	.11							
CV	3.28	4.88							
n	15	6							
Length of the upper molariform toothrow									
Mean	4.01	4.10			Sex	1	.032	1.40	.252
SD	.16	.14			Within	19	.023		
SE	.04	.06							
CV	3.99	3.41							
n	15	6							

Table 3.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Width of the widest molar									
Mean	1.73	1.78			Sex	1	.011	2.49	.131
SD	.06	.08			Within	19	.004		
SE	.02	.03							
CV	3.47	4.49							
n	15	6							
Greatest length of the mandible									
Mean	9.51	9.91			Sex	1	.747	8.03	.011
SD	.27	.37			Within	19	.093		
SE	.07	.14							
CV	2.84	3.73							
n	14	7							
Length of the mandibular toothrow									
Mean	5.64	5.77			Sex	1	.077	1.61	.219
SD	.17	.29			Within	19	.048		
SE	.05	.11							
CV	3.01	5.03							
n	14	7							
Length of the coronoid process									
Mean	2.47	2.63			Sex	1	.104	2.89	.109
SD	.19	.20			Within	16	.036		
SE	.06	.08							
CV	7.69	7.60							
n	11	7							

the study and had probably been used previously for an extended period (based upon the quantity of accumulated feces).

The Caatingas collection represents the largest analyzed sample of *Noctilio leporinus* from a single freely interbreeding population (see Davis, 1973). The results of a statistical analysis of 20 mensural morphological characters in *N. l. leporinus* are summarized in Table 4. Like the results reported by Davis (1973) for specimens from the Pacific versant of Chiapas, Mexico (*N. l. mastivus*), males tend to be more variable than females with consistently larger coefficients of variation. The sample means for males are larger than sample means for females for all 13 external characters analyzed, with statistically significant differences found for 10 of the variables. Males are statistically significantly different than, and larger on the average than, females for 15 of the 16 cranial characters. Although the sample mean for females is larger than that of males for the single character width of the widest molar, the difference is not statistically significant. *Noctilio l. leporinus* exhibits extreme sexual dimorphism with males consistently larger on the average than females.

Davis (1973) reported morphometric data from three localities (Upper Amazon Basin, Lower Amazon Basin, and the Guianas) within the range of *N. l. leporinus*. This facilitates comparison with the Caatingas population which is the northeastern-most collection locale of the species for which extensive morphometric data are available. The Caatingas population has larger mean values for four of the five morphometric characters reported by Davis (1973) and as such represents the most robust population within the subspecies. Further, among populations of *N. l. leporinus*, the Caatingas specimens are morphometrically more similar to specimens from the Upper Amazon Basin than to other populations.

Family Mormoopidae

Pteronotus davyi Gray, 1838

This aerial insectivore was rare in both Caatingas and Cerrado biomes. Of the three subspecies currently recognized, *P.d. davyi* is the appellation appropriate for specimens from the Northeast of Brazil (Smith, 1972).

Smith (1972) presented an analysis of systematic

Table 4.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Noctilio leporinus *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (P< .050) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	123.35	116.50	120.00	116.75	Sex	1	495.114	27.46	<.001
SD	3.84	4.57	—	5.38	Within	43	18.027		
SE	.86	1.02	—	2.69					
CV	3.11	3.92	—	4.61					
n	20	20	1	4					
Tail length									
Mean	27.60	25.30	28.00	25.75	Sex	1	56.400	11.52	.002
SD	2.54	2.06	—	1.50	Within	43	4.857		
SE	.57	.46	—	.75					
CV	9.20	8.14	—	5.83					
n	20	20	1	4					
Hindfoot length									
Mean	28.60	27.25	30.00	27.00	Sex	1	23.819	15.85	<.001
SD	1.27	1.16	—	1.41	Within	43	1.503		
SE	.29	.26	—	.71					
CV	4.44	4.26	—	5.22					
n	20	20	1	4					
Ear length									
Mean	28.45	28.55	28.00	27.50	Sex	1	.032	.02	.888
SD	1.57	.95	—	.58	Within	43	1.599		
SE	.35	.21	—	.29					
CV	5.52	3.33	—	2.11					
n	20	20	1	4					
Tragus length									
Mean	8.25	8.10	8.00	7.50	Sex	1	.635	1.98	.167
SD	.55	.55	—	.58	Within	43	.321		
SE	.12	.12	—	.29					
CV	6.67	6.79	—	7.73					
n	20	20	1	4					
Forearm length									
Mean	85.70	84.85	84.00	84.75	Sex	1	6.914	1.71	.199
SD	1.98	2.11	—	2.06	Within	43	4.053		
SE	.44	.47	—	1.03					
CV	2.31	2.49	—	2.43					
n	20	20	1	4					
Weight									
Mean	69.20	61.33	61.50	55.88	Sex	1	793.411	11.35	.002
SD	11.45	4.07	—	3.75	Within	43	69.895		
SE	2.56	.91	—	1.88					
CV	16.55	6.64	—	6.71					
n	20	20	1	4					
Length of digit one									
Mean	13.45	12.35	13.00	12.75	Sex	1	11.468	15.92	<.001
SD	1.00	.75	—	.50	Within	43	.720		
SE	.22	.17	—	.25					
CV	7.43	6.07	—	3.92					
n	20	20	1	4					

Table 4.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of digit three					
Mean	169.35	164.75	167.00	166.00	Sex	1	205.143	10.13	.003
SD	4.57	4.67	—	4.08	Within	43	20.250		
SE	1.02	1.04	—	2.04					
CV	2.70	2.83	—	2.46					
n	20	20	1	4					
				Length of digit four					
Mean	127.11	123.05	124.00	124.25	Sex	1	153.525	10.76	.002
SD	3.93	3.86	—	2.75	Within	43	14.266		
SE	.88	.86	—	1.38					
CV	3.09	3.14	—	2.21					
n	20	20	1	4					
				Length of digit five					
Mean	100.70	98.05	100.00	96.75	Sex	1	89.911	11.11	.002
SD	3.13	2.69	—	2.50	Within	43	8.093		
SE	.70	.60	—	1.25					
CV	3.11	2.74	—	2.58					
n	20	20	1	4					
				Tibia length					
Mean	41.55	39.80	41.00	40.00	Sex	1	32.006	17.52	<.001
SD	1.36	1.40	—	1.41	Within	43	1.827		
SE	.30	.31	—	.71					
CV	3.27	3.52	—	3.53					
n	20	20	1	4					
				Calcar length					
Mean	42.85	41.30	43.00	40.00	Sex	1	35.240	11.99	.001
SD	1.95	1.56	—	.82	Within	43	2.940		
SE	.44	.35	—	.41					
CV	4.55	3.78	—	2.05					
n	20	20	1	4					
				Greatest length of skull					
Mean	26.77	24.93	24.50	24.43	Sex	1	36.745	69.69	<.001
SD	.81	.47	—	.34	Within	43	.527		
SE	.18	.11	—	.17					
CV	3.03	1.89	—	1.39					
n	20	20	1	4					
				Condylobasal length					
Mean	24.33	23.16	23.60	23.23	Sex	1	14.265	103.22	<.001
SD	.43	.30	—	.29	Within	43	.138		
SE	.10	.07	—	.14					
CV	1.77	1.30	—	1.25					
n	20	20	1	4					
				Zygomatic breadth					
Mean	19.63	18.70	19.70	18.60	Sex	1	10.007	58.18	<.001
SD	.54	.31	—	.16	Within	43	.172		
SE	.12	.07	—	.08					
CV	2.75	1.66	—	.86					
n	20	20	1	4					

Table 4.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Postorbital constriction					
Mean	6.98	6.75	7.00	6.73	Sex	1	.641	15.23	<.001
SD	.16	.22	—	.36	Within	43	.042		
SE	.04	.05	—	.18					
CV	2.29	3.26	—	5.35					
n	20	20	1	4					
				Mastoid breadth					
Mean	18.34	16.89	16.60	16.80	Sex	1	20.727	38.13	<.001
SD	.95	.38	—	.20	Within	43	.544		
SE	.21	.09	—	.12					
CV	5.18	2.25	—	1.19					
n	20	20	1	3					
				Breadth of braincase					
Mean	13.77	13.47	14.00	13.78	Sex	1	1.161	17.85	<.001
SD	.22	.29	—	.25	Within	43	.065		
SE	.05	.07	—	.13					
CV	1.60	2.15	—	1.81					
n	20	20	1	4					
				Rostral breadth					
Mean	9.96	9.57	9.90	9.50	Sex	1	1.776	33.61	<.001
SD	.25	.20	—	.34	Within	43	.053		
SE	.06	.04	—	.17					
CV	2.51	2.09	—	3.58					
n	20	20	1	4					
				Height of braincase					
Mean	15.83	14.91	15.30	15.20	Sex	1	8.013	14.37	<.001
SD	1.05	.33	—	.29	Within	43	.558		
SE	.24	.07	—	.15					
CV	6.63	2.21	—	1.91					
n	20	20	1	4					
				Breadth across the upper molars					
Mean	12.64	12.28	12.30	12.08	Sex	1	1.560	34.72	<.001
SD	.22	.19	—	.19	Within	43	.045		
SE	.05	.04	—	.10					
CV	1.74	1.55	—	1.57					
n	20	20	1	4					
				Breadth across the upper canines					
Mean	9.44	8.73	9.60	8.65	Sex	1	5.974	109.89	<.001
SD	.26	.22	—	.13	Within	43	.054		
SE	.06	.05	—	.07					
CV	2.75	2.52	—	1.50					
n	20	20	1	4					
				Length of the maxillary toothrow					
Mean	10.62	10.25	10.30	10.08	Sex	1	1.610	41.22	<.001
SD	.22	.17	—	.10	Within	43	.039		
SE	.05	.04	—	.05					
CV	2.07	1.66	—	.99					
n	20	20	1	4					
				Length of the upper molariform toothrow					
Mean	8.71	8.50	8.70	8.58	Sex	1	.435	13.13	<.001
SD	.22	.14	—	.22	Within	43	.033		
SE	.05	.03	—	.11					
CV	2.53	1.65	—	2.56					
n	20	20	1	4					

Table 4.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Width of the widest molar					
Mean	3.29	3.31	3.00	3.23	Sex	1	.004	.22	.642
SD	.16	.10	—	.17	Within	43	.020		
SE	.04	.02	—	.09					
CV	4.86	3.02	—	5.26					
n	20	20	1	4					
				Greatest length of the mandible					
Mean	19.28	18.39	18.70	18.55	Sex	1	7.822	37.77	<.001
SD	.42	.49	—	.45	Within	43	.207		
SE	.09	.11	—	.23					
CV	2.18	2.66	—	2.43					
n	20	20	1	4					
				Length of the mandibular toothrow					
Mean	11.63	11.13	11.30	11.10	Sex	1	2.629	80.58	<.001
SD	.19	.18	—	.08	Within	43	.033		
SE	.04	.04	—	.04					
CV	1.63	1.62	—	.72					
n	20	20	1	4					
				Length of the coronoid process					
Mean	7.10	6.41	6.70	6.45	Sex	1	5.005	66.86	<.001
SD	.33	.23	—	.10	Within	43	.075		
SE	.07	.05	—	.05					
CV	4.65	3.59	—	1.55					
n	20	20	1	4					

relations within the family Mormoopidae, and considered to some extent, individual, secondary sexual, and geographic variation in the various species within the family. He stated that secondary sexual variation is apparent in *P. davyi* but noted that the number of characters that do differ between the sexes is related to geographic area. Data are combined from Caatingas and Cerrado populations because the samples from each site are small. Although geographic differences between areas can no longer be detected, this compromise facilitates the detection of sexual dimorphism in *P. davyi*. The results of the statistical analyses are shown in Table 5. Statistically significant secondary sexual variation is evident in three external characters in which the males are larger on the average than the females (ear length, tragus length, length of digit I); statistically significant secondary sexual variation is detected in only one external character in which the females are larger on the average than the males. None of the cranial characters exhibits statistically significant secondary sexual variation and a pattern in mean values is not observed for either external or cranial characters.

Family Phyllostomidae

Subfamily Phyllostominae

Micronycteris megalotis (Gray, 1842)

Of the four subspecies currently recognized, *M. m. megalotis* is the designation applicable to populations in Northeast Brazil (Jones and Carter, 1976). Mares et al. (1981) erroneously listed specimens of this species as *M. minuta* in their preliminary assessment of mammals from the Northeast of Brazil. This foliage gleaning insectivore was rare in both Caatingas and Cerrado biomes.

Numerous authors have reported measurements from *M. megalotis* (see Swanepoel and Genoways, 1979); however, only Miller (1898), Lima (1926), Cunha Vieira (1942) and Taddei (1975*a*) included specimens from Brazil. Taddei (1975*a*) reported information on individual variation, but did not perform statistical analyses in order to detect sexual dimorphism. Because samples were small from both Caatingas and Cerrado habitats, the data are combined for subsequent statistical analyses. The results are summarized in Table 6. Among the external

Table 5.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Pteronotus davyi *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (*P < .050*) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean	81.00		84.43	82.75	Sex	1	4.167	.42	.531
SD	—		2.44	4.19	Within	10	9.875		
SE	—		.92	2.10					
CV	—		2.89	5.06					
n	1		7	4					
				Tail length					
Mean	23.00		24.00	22.75	Sex	1	3.375	1.32	.278
SD	—		1.29	2.22	Within	10	2.563		
SE	—		.49	1.11					
CV	—		5.38	9.76					
n	1		7	4					
				Hindfoot length					
Mean	9.00		9.43	9.25	Sex	1	.042	.16	.699
SD	—		.54	.50	Within	10	.263		
SE	—		.20	.25					
CV	—		5.73	5.41					
n	1		7	4					
				Ear length					
Mean	17.00		17.43	16.00	Sex	1	5.042	13.01	.005
SD	—		.54	.82	Within	10	.388		
SE	—		.20	.41					
CV	—		3.10	5.13					
n	1		7	4					
				Tragus length					
Mean	6.00		7.00	5.75	Sex	1	3.375	6.00	.034
SD	—		.82	.50	Within	10	.563		
SE	—		.31	.25					
CV	—		11.71	8.70					
n	1		7	4					
				Forearm length					
Mean	48.00		50.86	51.00	Sex	1	.667	.42	.533
SD	—		1.07	.82	Within	10	1.600		
SE	—		.40	.41					
CV	—		2.10	1.61					
n	1		7	4					
				Weight					
Mean	12.00		12.14	13.25	Sex	1	3.375	10.80	.008
SD	—		.38	.87	Within	10	.313		
SE	—		.14	.43					
CV	—		3.13	6.57					
n	1		7	4					
				Length of digit one					
Mean	8.00		8.43	8.00	Sex	1	.375	2.00	.188
SD	—		.54	0	Within	10	.188		
SE	—		.20	0					
CV	—		6.41	0					
n	1		7	4					

Table 5.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	78.00		78.86	80.25	Sex	1	6.000	1.75	.215
SD	—		2.04	1.71	Within	10	3.435		
SE	—		.77	.85					
CV	—		2.59	2.13					
n	1		7	4					
Length of digit four									
Mean	56.00		58.28	59.00	Sex	1	2.677	1.33	.275
SD	—		1.50	.82	Within	10	2.000		
SE	—		.57	.41					
CV	—		2.57	1.39					
n	1		7	4					
Length of digit five									
Mean	57.00		58.29	59.00	Sex	1	2.042	1.59	.237
SD	—		1.25	.82	Within	10	1.288		
SE	—		.48	.41					
CV	—		2.14	1.40					
n	1		7	4					
Tibia length									
Mean	21.00		21.14	21.25	Sex	1	.042	.07	.791
SD	—		.90	.50	Within	10	.563		
SE	—		.34	.25					
CV	—		4.26	2.35					
n	1		7	4					
Calcar length									
Mean	22.00		21.29	22.00	Sex	1	1.042	1.77	.213
SD	—		.76	.82	Within	10	.588		
SE	—		.29	.41					
CV	—		3.57	3.73					
n	1		7	4					
Greatest length of skull									
Mean	15.80		15.97	15.70	Sex	1	.167	2.78	.127
SD	—		.24	.27	Within	10	.060		
SE	—		.09	.14					
CV	—		1.50	1.72					
n	1		7	4					
Condylobasal length									
Mean	15.10		15.44	15.30	Sex	1	.027	.36	.562
SD	—		.30	.18	Within	10	.074		
SE	—		.11	.09					
CV	—		1.94	1.18					
n	1		7	4					
Zygomatic breadth									
Mean	9.60		9.70	9.60	Sex	1	.020	.89	.367
SD	—		.18	.08	Within	10	.023		
SE	—		.07	.04					
CV	—		1.86	.83					
n	1		7	4					

Table 5.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	4.00		4.04	3.93	Sex	1	.034	3.91	.076
SD	—		.10	.10	Within	10	.009		
SE	—		.04	.05					
CV	—		2.48	2.54					
n	1		7	4					
Mastoid breadth									
Mean	9.50		9.54	9.40	Sex	1	.050	1.69	.223
SD	—		.18	.18	Within	10	.030		
SE	—		.07	.09					
CV	—		1.89	1.91					
n	1		7	4					
Breadth of braincase									
Mean	8.50		8.51	8.35	Sex	1	.707	3.54	.089
SD	—		.12	.19	Within	10	.020		
SE	—		.05	.10					
CV	—		1.41	2.28					
n	1		7	4					
Rostral breadth									
Mean	5.10		5.21	5.13	Sex	1	.015	1.40	.265
SD	—		.12	.05	Within	10	.011		
SE	—		.05	.03					
CV	—		2.30	.97					
n	1		7	4					
Height of braincase									
Mean	10.00		9.96	9.73	Sex	1	.150	3.70	.083
SD	—		.24	.15	Within	10	.041		
SE	—		.09	.08					
CV	—		2.41	1.54					
n	1		7	4					
Breadth across the upper molars									
Mean	6.60		6.60	6.60	Sex	1	.000	0	1.000
SD	—		.14	.08	Within	10	.014		
SE	—		.05	.04					
CV	—		2.12	1.21					
n	1		7	4					
Breadth across the upper canines									
Mean	5.30		5.49	5.50	Sex	1	.004	.16	.700
SD	—		.15	.16	Within	10	.024		
SE	—		.06	.08					
CV	—		2.73	2.91					
n	1		7	4					
Length of the maxillary toothrow									
Mean	7.00		7.16	7.05	Sex	1	.020	.62	.449
SD	—		.21	.13	Within	10	.033		
SE	—		.08	.07					
CV	—		2.93	1.84					
n	1		7	4					
Length of the upper molariform toothrow									
Mean	5.40		5.64	5.68	Sex	1	.010	.76	.402
SD	—		.05	.15	Within	10	.014		
SE	—		.02	.08					
CV	—		.89	2.64					
n	1		7	4					

Table 5.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Width of the widest molar					
Mean	1.90		1.87	1.93	Sex	1	.007	1.07	.326
SD	—		.08	.10	Within	10	.006		
SE	—		.03	.05					
CV	—		4.28	5.18					
n	1		7	4					
				Greatest length of the mandible					
Mean	12.70		12.69	12.70	Sex	1	.000	.01	.920
SD	—		.23	.16	Within	10	.039		
SE	—		.09	.08					
CV	—		1.81	1.26					
n	1		7	4					
				Length of the mandibular toothrow					
Mean	7.40		7.54	7.50	Sex	1	.002	.14	.711
SD	—		.08	.14	Within	10	.012		
SE	—		.03	.07					
CV	—		1.06	1.87					
n	1		7	4					
				Length of the coronoid process					
Mean	3.00		3.14	3.15	Sex	1	.002	.37	.556
SD	—		.05	.06	Within	10	.005		
SE	—		.02	.03					
CV	—		1.59	1.90					
n	1		7	4					

characters, only tragus length exhibits statistically significant secondary sexual variation and no trend is evident when comparing female and male mean values. Nevertheless, the sample means for males are larger than those for females for 15 of the 16 cranial characters with differences in cranial characters statistically significant for mastoid breadth, width of the widest molar, length from the canine to the last molar in the mandible and length of the coronoid process. It appears then, that the sample means for males are consistently larger than those for females when cranial characters are considered but that similar trends are not apparent for external characteristics. The evidence from the Northeast of Brazil suggests the possibility of sexual dimorphism for *M. m. megalotis,* however, larger samples are required to make such a statement with complete statistical confidence.

Micronycteris minuta (Gervais, 1856)

Specimens in this monotypic species are listed as *Micronycteris* sp. by Mares et al. (1981). It is a foliage gleaning insectivore that was rare in the Caatingas, where it was most frequently caught near lajeiros or serrotes. *M. minuta* is also rare on the Chapada do Araripe.

Measurements of *M. minuta* have not appeared frequently in the literature (see Swanepoel and Genoways, 1979); however, Dobson (1878), Andersen (1906), G. M. Allen (1908), and Cunha Vieira (1942) included Brazilian specimens in their work. The only comparative morphometric work on the species was done by Sanborn (1949); he suggested that Colombian specimens are smaller than specimens from Brazil, however, his analysis was not conclusive.

The existence of sexual dimorphism was examined via the analysis of variance for specimens from the Northeast of Brazil. Specimens from the Caatingas and Chapada were combined due to small sample size and the results are shown in Table 7. None of the cranial characters and only two external characters exhibit statistically significant sexual variation. Because there is no apparent pattern in the relationship between male and female mean values either, there is little reason for considering specimens of *M. minuta* sufficiently dimorphic to war-

Table 6.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Micronycteris megalotis *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (*P *< .050) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Total length				
Mean	59.86	60.00	58.67		Sex	1	.714	.06	.805
SD	2.91	2.00	5.86		Within	12	11.208		
SE	1.10	1.00	3.38						
CV	4.86	3.33	9.99						
n	7	4	3						
					Tail length				
Mean	13.57	13.00	14.67		Sex	1	2.314	.96	.346
SD	1.40	1.41	2.08		Within	12	2.408		
SE	.53	.71	1.20						
CV	10.32	10.85	14.17						
n	7	4	3						
					Hindfoot length				
Mean	8.14	8.00	8.00		Sex	1	.029	.12	.737
SD	.38	0	1.00		Within	12	.242		
SE	.14	0	.58						
CV	4.67	0	12.50						
n	7	4	3						
					Ear length				
Mean	20.86	21.25	20.33		Sex	1	.864	2.14	.169
SD	.69	.50	.58		Within	12	.404		
SE	.26	.25	.33						
CV	3.31	2.35	2.85						
n	7	4	3						
					Tragus length				
Mean	7.57	6.75	8.00		Sex	1	2.579	10.86	.006
SD	.53	.50	0		Within	12	.238		
SE	.20	.25	0						
CV	7.13	7.41	0						
n	7	4	3						
					Forearm length				
Mean	34.29	34.75	34.33		Sex	1	.579	1.01	.334
SD	.76	.50	1.16		Within	12	.571		
SE	.29	.25	.67						
CV	2.22	1.44	3.38						
n	7	4	3						
					Weight				
Mean	5.93	5.75	6.67		Sex	1	.457	.75	.402
SD	.54	.29	1.44		Within	12	.606		
SE	.20	.14	.83						
CV	9.11	5.04	21.59						
n	7	4	3						
					Length of digit one				
Mean	8.43	8.25	9.00		Sex	1	.350	1.33	.271
SD	.54	.50	0		Within	12	.263		
SE	.20	.25	0						
CV	6.41	6.06	0						
n	7	4	3						

Table 6.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	61.00	62.50	63.67		Sex	1	1.400	.24	.635
SD	2.00	1.00	3.79		Within	12	5.883		
SE	.76	.50	2.19						
CV	3.28	1.60	5.95						
n	7	4	3						
Length of digit four									
Mean	46.57	46.75	47.00		Sex	1	.007	.00	.947
SD	1.40	1.26	1.00		Within	12	1.571		
SE	.53	.63	.58						
CV	3.01	2.70	2.13						
n	7	4	3						
Length of digit five									
Mean	47.71	48.00	48.33		Sex	1	.029	.01	.918
SD	1.80	.82	2.08		Within	12	2.575		
SE	.68	.41	1.20						
CV	3.77	1.71	4.30						
n	7	4	3						
Tibia length									
Mean	16.71	15.75	16.67		Sex	1	2.579	2.41	.147
SD	1.25	.50	1.16		Within	12	1.071		
SE	.47	.25	.67						
CV	7.48	3.17	6.96						
n	7	4	3						
Calcar length									
Mean	11.00	10.75	10.67		Sex	1	.064	.10	.756
SD	1.00	.50	.58		Within	12	.638		
SE	.38	.25	.33						
CV	9.09	4.65	5.44						
n	7	4	3						
Noseleaf length									
Mean	6.42	7.00	7.00		Sex	1	.457	.86	.373
SD	.79	0	1.00		Within	12	.533		
SE	.30	0	.58						
CV	12.31	0	14.29						
n	7	4	3						
Greatest length of skull									
Mean	18.18	17.73	18.17		Sex	1	.568	2.81	.122
SD	.44	.31	.70		Within	11	.202		
SE	.18	.16	.41						
CV	2.42	1.75	3.85						
n	6	4	3						
Condylobasal length									
Mean	16.17	15.58	16.20		Sex	1	1.006	4.49	.058
SD	.57	.13	.62		Within	11	.224		
SE	.23	.06	.36						
CV	3.53	.83	3.83						
n	6	4	3						
Zygomatic breadth									
Mean	8.88	8.67	8.90		Sex	1	.106	1.86	.206
SD	.33	.12	.17		Within	9	.057		
SE	.15	.07	.10						
CV	3.72	1.38	1.91						
n	5	3	3						

Table 6.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	3.85	3.78	3.77		Sex	1	.006	.30	.592
SD	.18	.05	.15		Within	10	.020		
SE	.07	.03	.09						
CV	4.68	1.32	3.98						
n	6	4	3						
Mastoid breadth									
Mean	8.54	8.33	8.70		Sex	1	.202	5.20	.046
SD	.17	.13	.30		Within	10	.039		
SE	.08	.06	.17						
CV	1.99	1.56	3.45						
n	5	4	3						
Breadth of braincase									
Mean	7.38	7.35	7.63		Sex	1	.042	1.03	.334
SD	.16	.13	.25		Within	10	.041		
SE	.07	.07	.15						
CV	2.17	1.77	3.28						
n	5	4	3						
Rostral breadth									
Mean	3.26	3.23	3.27		Sex	1	.004	.14	.711
SD	.13	.17	.23		Within	12	.024		
SE	.05	.09	.13						
CV	3.99	5.26	7.03						
n	7	4	3						
Height of braincase									
Mean	9.48	9.35	9.43		Sex	1	.034	.44	.522
SD	.34	.24	.31		Within	11	.086		
SE	.14	.12	.18						
CV	3.59	2.57	3.29						
n	6	4	3						
Breadth across the upper molars									
Mean	6.02	5.85	5.93		Sex	1	.053	3.28	.097
SD	.08	.13	.21		Within	11	.016		
SE	.03	.07	.12						
CV	1.33	2.22	3.54						
n	6	4	3						
Breadth across the upper canines									
Mean	3.15	3.20	3.17		Sex	1	.006	.49	.498
SD	.11	.12	.12		Within	11	.011		
SE	.04	.06	.07						
CV	3.49	3.75	3.79						
n	6	4	3						
Length of the maxillary toothrow									
Mean	6.80	6.60	6.93		Sex	1	.165	1.02	.333
SD	.55	.08	.21		Within	12	.162		
SE	.21	.04	.12						
CV	8.09	1.21	3.03						
n	7	4	3						
Length of the upper molariform toothrow									
Mean	5.73	5.50	5.97		Sex	1	.179	1.12	.310
SD	.54	.10	.15		Within	12	.159		
SE	.20	.05	.09						
CV	9.42	1.82	2.51						
n	7	4	3						

Table 6.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Width of the widest molar				
Mean	1.69	1.55	1.73		Sex	1	.064	8.57	.013
SD	.09	.10	.06		Within	12	.008		
SE	.03	.05	.03						
CV	5.33	6.45	3.47						
n	7	4	3						
					Greatest length of the mandible				
Mean	11.79	11.40	11.73		Sex	1	.391	2.93	.113
SD	.44	.18	.42		Within	12	.113		
SE	.17	.09	.24						
CV	3.73	1.58	3.58						
n	7	4	3						
					Length of the mandibular toothrow				
Mean	7.50	7.18	7.50		Sex	1	.302	5.77	.033
SD	.29	.10	.20		Within	12	.052		
SE	.11	.05	.12						
CV	3.87	1.39	2.67						
n	7	4	3						
					Length of the coronoid process				
Mean	3.87	3.68	3.93		Sex	1	.132	10.13	.008
SD	.14	.05	.12		Within	12	.013		
SE	.05	.03	.07						
CV	3.62	1.36	3.05						
n	7	4	3						

Table 7.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Micronycteris minuta *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (*$P < .050$*) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Total length				
Mean	54.75	56.00	63.00		Sex	1	10.971	.70	.427
SD	.50	1.00	1.73		Within	8	15.679		
SE	.25	.58	1.00						
CV	.91	1.79	2.74						
n	4	3	3						
					Tail length				
Mean	11.25	12.00	12.33		Sex	1	.171	.12	.738
SD	.96	1.00	1.53		Within	8	1.429		
SE	.48	.58	.88						
CV	8.53	8.33	12.41						
n	4	3	3						
					Hindfoot length				
Mean	8.50	8.67	8.67		Sex	1	.019	.06	.807
SD	.58	.58	.58		Within	8	.298		
SE	.29	.33	.33						
CV	6.82	6.70	6.69						
n	4	3	3						

Table 7.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Ear length				
Mean	18.50	19.33	26.00		Sex	1	.476	.28	.610
SD	1.00	.58	4.58		Within	8	1.691		
SE	.50	.33	2.65						
CV	5.41	3.00	17.62						
n	4	3	3						
					Tragus length				
Mean	7.00	7.00	7.00						
SD	0	0	0						
SE	0	0	0						
CV	0	0	0						
n	4	3	3						
					Forearm length				
Mean	32.75	34.00	34.00		Sex	1	1.071	1.15	.314
SD	.96	0	1.00		Within	8	.929		
SE	.48	0	.58						
CV	2.93	0	2.94						
n	4	3	3						
					Weight				
Mean	5.75	6.83	5.67		Sex	1	2.630	5.85	.042
SD	.29	1.26	.29		Within	8	.449		
SE	.14	.73	.17						
CV	5.04	18.45	5.11						
n	4	3	3						
					Length of digit one				
Mean	6.25	7.00	6.67		Sex	1	.686	3.20	.111
SD	.50	0	.58		Within	8	.214		
SE	.25	0	.33						
CV	8.00	0	8.70						
n	4	3	3						
					Length of digit three				
Mean	54.50	57.33	56.67		Sex	1	7.619	2.99	.122
SD	.58	2.31	.58		Within	8	2.548		
SE	.29	1.33	.33						
CV	1.06	4.03	1.02						
n	4	3	3						
					Length of digit four				
Mean	41.50	43.33	42.67		Sex	1	3.733	1.45	.264
SD	1.29	2.52	.58		Within	8	2.583		
SE	.65	1.45	.33						
CV	3.11	5.82	1.36						
n	4	3	3						
					Length of digit five				
Mean	41.50	44.00	42.67		Sex	1	8.400	5.60	.046
SD	1.00	1.73	.58		Within	8	1.500		
SE	.50	1.00	.33						
CV	3.77	3.93	1.36						
n	4	3	3						
					Tibia length				
Mean	15.00	15.33	16.00		Sex	1	.019	.02	.896
SD	.82	1.16	1.00		Within	8	1.048		
SE	.41	.67	.58						
CV	5.47	7.57	6.25						
n	4	3	3						

Table 7.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Calcar length									
Mean	8.75	9.00	9.67		Sex	1	.043	.04	.849
SD	.96	1.00	1.16		Within	8	1.107		
SE	.48	.58	.67						
CV	10.97	11.11	12.00						
n	4	3	3						
Noseleaf length									
Mean	5.25	5.33	5.33		Sex	1	.005	.02	.896
SD	.50	.58	.58		Within	8	.262		
SE	.25	.33	.33						
CV	9.52	10.88	10.88						
n	4	3	3						
Greatest length of skull									
Mean	16.80	16.77	16.95		Sex	1	.014	.12	.735
SD	.41	.32	.21		Within	7	.112		
SE	.20	.19	.15						
CV	2.44	1.91	1.24						
n	4	3	2						
Condylobasal length									
Mean	14.83	14.93	15.00		Sex	1	.005	.10	.763
SD	.29	.15	.14		Within	7	.051		
SE	.14	.09	.10						
CV	1.96	1.00	.93						
n	4	3	2						
Zygomatic breadth									
Mean	7.93	8.10	8.00		Sex	1	.030	4.00	.116
SD	.96	.14	—		Within	4	.008		
SE	.03	.10	—						
CV	.76	1.73	—						
n	3	2	1						
Postorbital constriction									
Mean	3.75	3.90	4.03		Sex	1	.002	.05	.835
SD	.17	.17	.06		Within	8	.037		
SE	.09	.10	.03						
CV	4.53	4.36	1.49						
n	4	3	3						
Mastoid breadth									
Mean	8.15	8.18	8.40		Sex	1	.009	.19	.673
SD	.24	.15	.14		Within	7	.046		
SE	.12	.09	.10						
CV	2.94	1.84	1.67						
n	4	3	2						
Breadth of braincase									
Mean	7.25	7.23	7.40		Sex	1	.005	.18	.685
SD	.13	.21	.14		Within	7	.028		
SE	.06	.12	.10						
CV	1.79	2.90	1.89						
n	4	3	2						
Rostral breadth									
Mean	2.98	2.90	3.03		Sex	1	.021	4.20	.075
SD	.05	.10	.06		Within	8	.005		
SE	.03	.06	.03						
CV	1.68	3.45	1.98						
n	4	3	3						

Table 7.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Height of braincase									
Mean	8.90	8.93	8.90		Sex	1	.002	.04	.838
SD	.29	.21	0		Within	7	.050		
SE	.15	.21	0						
CV	3.26	2.35	0						
n	4	3	2						
Breadth across the upper molars									
Mean	5.03	5.07	5.27		Sex	1	.008	.46	.518
SD	.05	.06	.12		Within	8	.018		
SE	.03	.03	.07						
CV	.99	1.18	2.28						
n	4	3	3						
Breadth across the upper canines									
Mean	2.73	2.67	2.87		Sex	1	.030	2.50	.153
SD	.05	.06	.15		Within	8	.012		
SE	.03	.03	.09						
CV	1.83	2.25	5.23						
n	4	3	3						
Length of the maxillary toothrow									
Mean	5.75	5.97	5.73		Sex	1	.015	5.14	.053
SD	.06	.25	.12		Within	8	.021		
SE	.03	.15	.07						
CV	1.04	4.19	2.09						
n	4	3	3						
Length of the upper molariform toothrow									
Mean	4.88	4.90	4.90		Sex	1	.000	.03	.863
SD	.10	.17	.10		Within	8	.014		
SE	.05	.10	.06						
CV	2.05	3.47	2.04						
n	4	3	3						
Width of the widest molar									
Mean	1.38	1.43	1.33		Sex	1	.012	4.10	.078
SD	.05	.06	.06		Within	8	.003		
SE	.03	.03	.03						
CV	3.62	4.20	4.51						
n	4	3	3						
Greatest length of the mandible									
Mean	10.43	10.43	10.47		Sex	1	.000	.02	.896
SD	.10	.06	.15		Within	8	.011		
SE	.05	.03	.09						
CV	.96	.58	1.43						
n	4	3	3						
Length of the mandibular toothrow									
Mean	6.28	6.27	6.05		Sex	1	.009	.27	.617
SD	.17	.12	.21		Within	7	.032		
SE	.09	.07	.15						
CV	2.71	1.91	3.47						
n	4	3	2						
Length of the coronoid process									
Mean	3.05	3.10	3.27		Sex	1	.004	.26	.622
SD	.06	.10	.06		Within	8	.015		
SE	.03	.06	.03						
CV	1.97	3.23	1.83						
n	4	3	3						

rant analyzing males and females separately in future analyses.

Tonatia bidens (Spix, 1823)

T. b. bidens is the only extant subspecies currently recognized (Jones and Carter, 1976). This foliage gleaning insectivore was rare in the Caatingas where it was only captured on serrotes; it was apparently absent from the Chapada do Araripe.

Few mensural data are reported in the literature for *T. bidens.* Dobson (1879), Lima (1926), Sanborn (1936), Cunha Vieira (1942), and Goodwin (1942) reported measurements from Brazilian specimens. Only selected measurements (after Swanepoel and Genoways, 1979) are reported here for the two adult males and one adult female captured in the Caatingas (total length, 85, 96, 93; tail length, 18, 19, 18; hindfoot length, 14, 14, 13; ear length, 32, 30, 33; greatest length of skull, 27.4, 27.3, 27.1; condylobasal length, 24.1, 23.1, 23.6; zygomatic breadth, 14.3, 14.0, 14.0; postorbital constriction, 5.7, 5.3, 5.2; breadth of braincase, 11.0, 10.7, 10.7; length of the maxillary toothrow, 9.8, 9.8, 9.5; breadth across the upper molars, 8.6, 8.8, 8.5).

Tonatia brasiliense (Peters, 1866)

Jones and Carter (1976) consider *T. brasiliense* to be monotypic; however, if one includes specimens of *T. venezuelae, T. minuta,* and *T. nicaraguae* within this taxon as is frequently done (Gardner, 1976; Koopman, 1978), then the species is, no doubt, polytypic. It was uncommon in the Caatingas but was consistently captured on serrotes or in Caatinga Alta habitats. *T. brasiliense* was absent from all habitats on Chapada do Araripe.

Most of the recorded measurements for *T. brasiliense* were derived from Peters (1866) original description of the holotype. Goodwin (1942) presented data on two more specimens from Brazil and Gardner (1976) presented data on two additional specimens from Peru. Samples from the Caatingas are too small to allow statistical analyses, therefore data are reported here on a selected set of mensural characters (after Swanepoel and Genoways, 1979). The first figure represents the mean value derived from six adult females, whereas the second figure represents the mean value derived from two adult males (total length, 69.8, 75.0; tail length, 9.2, 11.0; hindfoot length, 9.8, 10.0; ear length, 23.8, 22.0; greatest length of skull, 20.44, 19.95; condylobasal length, 17.86, 17.40; zygomatic breadth, 10.30, 9.95; postorbital constriction, 3.23, 3.25; breadth of braincase, 8.42, 8.25; length of maxillary toothrow, 8.18, 8.10; breadth across the upper molars, 6.62, 6.45).

Tonatia silvicola (D'Orbigny, 1836)

Two subspecies are currently recognized in this taxon; *T. s. laephotis* is the designation appropriate for specimens from northeastern Brazil (Jones and Carter, 1976). This foliage gleaning insectivore is absent from the Chapada do Araripe, and its occurrence in the Caatingas was primarily restricted to serrotes. All but three of the specimens from the Northeast of Brazil listed by Mares et al. (1981) as *T. bidens* were actually *T. silvicola.* Based upon netting records for adult specimens from the duration of this study, the sex ratio was not equal in this species (Bionomial test, $P < .05$); approximately 30% of the 47 captured adult individuals were males.

Swanepoel and Genoways (1979) summarized the sources of recorded measurements for *T. silvicola*; Peters (1865), Dobson (1878), Cunha Vieira (1942), and Goodwin (1942) are noteworthy in that listing because they have included Brazilian specimens in their work. Statistical analyses of individual variation have not been done nor has the existence of sexual dimorphism been considered in the literature. Samples are sufficiently large from the Caatingas to determine individual variation and ascertain with confidence the degree of sexual dimorphism present in a population of *T. silvicola.* The results of the statistical analysis are presented in Table 8. The sample means for males are larger than the sample means for females for 24 of the 30 characters examined. Statistically significant secondary sexual variation is revealed for two external characters (ear length and weight) and six cranial characters (greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, height of the braincase, and length in the mandible from the canine to the last molar). Statistical significance is not found in the variables that had larger sample mean values for females. *T. silvicola* is clearly dimorphic for cranial characters with males larger than females.

Mimon crenulatum (E. Geoffroy, 1819)

Jones and Carter (1976) recognize four subspecies in this taxon, whereas Koopman (1978) includes a fifth form. In either case, *M. c. crenulatum* is the designation properly applied to specimens from northeastern Brazil. This foliage gleaning insectivore was found exclusively in Caatinga Alta habitats.

A paucity of data exists concerning the morphometrics of *M. crenulatum* (see Swanepoel and Gen-

Table 8.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Tonatia silvicola *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	97.85	97.58			Sex	1	.660	.07	.799
SD	3.34	3.12			Within	47	10.095		
SE	.93	.52							
CV	3.41	3.20							
n	13	36							
Tail length									
Mean	17.69	17.69			Sex	1	.000	.00	.998
SD	2.50	2.04			Within	47	4.690		
SE	.69	.34							
CV	14.13	11.53							
n	13	36							
Hindfoot length									
Mean	14.62	14.69			Sex	1	.060	.11	.747
SD	.51	.82			Within	47	.568		
SE	.14	.14							
CV	3.49	5.58							
n	13	36							
Ear length									
Mean	29.62	28.81			Sex	1	6.264	7.60	.008
SD	1.12	.82			Within	47	.824		
SE	.31	.14							
CV	3.78	2.85							
n	13	36							
Tragus length									
Mean	11.69	11.86			Sex	1	.272	.28	.597
SD	1.38	.80			Within	47	.959		
SE	.38	.13							
CV	11.80	6.74							
n	13	36							
Forearm length									
Mean	58.23	57.58			Sex	1	4.004	3.30	.076
SD	1.42	.97			Within	47	1.214		
SE	.40	.16							
CV	2.44	1.68							
n	13	36							
Weight									
Mean	33.85	31.79			Sex	1	40.314	5.06	.029
SD	3.07	2.73			Within	47	7.966		
SE	.85	.46							
CV	9.07	8.59							
n	13	36							
Length of digit one									
Mean	15.08	14.94			Sex	1	.168	.23	.637
SD	.76	.89			Within	47	.741		
SE	.21	.15							
CV	5.04	5.96							
n	13	36							

Table 8.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	106.54	106.00			Sex	1	2.769	.65	.423
SD	2.63	1.82			Within	47	4.239		
SE	.73	.30							
CV	2.47	1.72							
n	13	36							
Length of digit four									
Mean	80.46	79.81			Sex	1	4.110	1.26	.267
SD	2.37	1.56			Within	47	3.253		
SE	.66	.26							
CV	2.95	1.95							
n	13	36							
Length of digit five									
Mean	81.39	80.47			Sex	1	7.951	3.06	.087
SD	2.40	1.23			Within	47	2.597		
SE	.67	.21							
CV	2.95	1.53							
n	13	36							
Tibia length									
Mean	27.08	27.25			Sex	1	.286	.25	.619
SD	1.66	.77			Within	47	1.142		
SE	.46	.13							
CV	6.13	2.83							
n	13	36							
Calcar length									
Mean	18.54	17.78			Sex	1	5.527	3.35	.073
SD	1.33	1.27			Within	47	1.648		
SE	.37	.21							
CV	7.17	7.14							
n	13	36							
Noseleaf length									
Mean	6.54	6.33			Sex	1	.402	1.68	.201
SD	.52	.48			Within	47	.239		
SE	.14	.08							
CV	7.95	7.58							
n	13	36							
Greatest length of skull									
Mean	27.80	27.32			Sex	1	2.180	7.93	.007
SD	.54	.52			Within	47	.275		
SE	.15	.09							
CV	1.94	1.90							
n	13	36							
Condylobasal length									
Mean	24.31	23.84			Sex	1	2.050	14.56	<.001
SD	.50	.32			Within	47	.141		
SE	.14	.05							
CV	2.06	1.34							
n	13	36							
Zygomatic breadth									
Mean	13.68	13.47			Sex	1	.412	6.82	.012
SD	.24	.25			Within	45	.060		
SE	.07	.04							
CV	1.75	1.86							
n	13	34							

Table 8.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	6.00	6.00			Sex	1	.000	.00	.967
SD	.15	.22			Within	47	.042		
SE	.04	.04							
CV	2.50	3.67							
n	13	36							
Mastoid breadth									
Mean	13.49	13.27			Sex	1	.454	7.42	.009
SD	.20	.26			Within	46	.061		
SE	.05	.05							
CV	1.48	1.96							
n	13	35							
Breadth of braincase									
Mean	11.03	11.10			Sex	1	.042	.92	.343
SD	.19	.22			Within	47	.046		
SE	.05	.04							
CV	1.72	1.98							
n	13	36							
Rostral breadth									
Mean	5.99	5.92			Sex	1	.047	1.68	.201
SD	.19	.16			Within	47	.028		
SE	.05	.03							
CV	3.17	2.70							
n	13	36							
Height of braincase									
Mean	13.96	13.73			Sex	1	.534	6.65	.013
SD	.32	.27			Within	47	.080		
SE	.09	.05							
CV	2.29	1.97							
n	13	36							
Breadth across the upper molars									
Mean	8.90	8.84			Sex	1	.030	.89	.349
SD	.22	.17			Within	47	.033		
SE	.06	.03							
CV	2.47	1.92							
n	13	36							
Breadth across the upper canines									
Mean	6.12	6.05			Sex	1	.055	2.00	.164
SD	.15	.17			Within	47	.028		
SE	.04	.03							
CV	2.45	2.81							
n	13	36							
Length of the maxillary toothrow									
Mean	10.12	10.03			Sex	1	.092	3.69	.061
SD	.21	.14			Within	47	.025		
SE	.06	.02							
CV	2.08	1.40							
n	13	36							
Length of the upper molariform toothrow									
Mean	7.96	7.93			Sex	1	.011	.45	.507
SD	.16	.15			Within	47	.024		
SE	.04	.03							
CV	2.01	1.89							
n	13	36							

Table 8.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Width of the widest molar					
Mean	2.42	2.45			Sex	1	.010	1.12	.296
SD	.10	.09			Within	47	.009		
SE	.03	.02							
CV	4.13	3.67							
n	13	36							
				Greatest length of the mandible					
Mean	18.10	17.98			Sex	1	.130	1.33	.256
SD	.34	.31			Within	47	.098		
SE	.09	.05							
CV	1.88	1.72							
n	13	36							
				Length of the mandibular toothrow					
Mean	11.29	11.09			Sex	1	.366	6.16	.017
SD	.22	.25			Within	47	.059		
SE	.06	.04							
CV	1.95	2.25							
n	13	36							
				Length of the coronoid process					
Mean	7.35	7.25			Sex	1	.098	2.27	.139
SD	.21	.21			Within	47	.043		
SE	.06	.03							
CV	2.86	2.90							
n	13	36							

oways, 1979). Peters (1866), Dobson (1878), Thomas (1903), Cunha Vieira (1942), and Handley (1960) included specimens from Brazil in their work, but statistical analyses were not attempted. Samples from the Caatingas are sufficiently large to perform statistical analyses; the results are shown in Table 9. Only a single character, condylobasal length, exhibits statistically significant secondary sexual variation and trends in the relationship of male and female mean values could not be detected for the other variables. The data cannot substantiate the presence of sexual dimorphism in the Caatingas population of *M. c. crenulatum,* but this failure may be due to small sample sizes.

Phyllostomus discolor (Wagner, 1843)

Power and Tamsitt (1973) recently suggested that *P. discolor* is a monotypic species because there is little morphometric basis for distinguishing between the two presently recognized subspecies. In keeping with current usage, however, *P. d. discolor* is the appropriate appellation for populations east of the Andes (Jones and Carter, 1976) and would thus apply to specimens from northeastern Brazil. Although primarily frugivorous, at least part of the year *P. d. discolor* consumed nectar, pollen, flower parts, and insects; thus, it should be considered omnivorous. Based upon pollen loads from Cerrado specimens, *P. d. discolor* was an important pollinator of *Caryocar coriaceum.* In fact, the number of captured specimens of this species increased fourfold during months when *C. coriaceum* flowered; this strongly suggests recruitment from surrounding areas as preferred resources became abundant on the Chapada. *P. d. discolor* was widespread and abundant on the Chapada do Araripe but restricted for the most part to banana and mango orchards in the Caatingas. Thirty-eight percent of the 26 captured adult specimens from the Caatingas were males; similarly, 36% of the 180 captured adult specimens from the Chapada do Araripe were males. In the Cerrado, *P. d. discolor* exhibited a significantly unequal sex ratio (Binomial Test, $P < .01$). Samples from the Caatingas failed to exhibit a significantly unequal sex ratio (Binomial Test, $P > .05$), but this may be attributed in part to the small sample size available from this study. Numerous authors have reported measurements for *P. discolor* (see Swanepoel and Genoways, 1979) but only Peters (1865), Cunha Vieira (1942), Power and Tamsitt

Table 9.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Mimon crenulatum *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	79.00	84.50			Sex	1	51.857	3.99	.102
SD	4.36	3.00			Within	5	13.000		
SE	2.52	1.50							
CV	5.52	3.55							
n	3	4							
Tail length									
Mean	23.00	22.00			Sex	1	1.714	.36	.616
SD	1.73	2.45			Within	5	4.800		
SE	1.00	1.23							
CV	7.52	11.14							
n	3	4							
Hindfoot length									
Mean	10.00	9.75			Sex	1	.107	.71	.437
SD	0	.50			Within	5	.150		
SE	0	.25							
CV	0	5.13							
n	3	4							
Ear length									
Mean	26.00	26.50			Sex	1	.429	2.14	.203
SD	0	.58			Within	5	.200		
SE	0	.29							
CV	0	2.19							
n	3	4							
Tragus length									
Mean	11.67	11.25			Sex	1	.298	.16	.707
SD	1.53	1.26			Within	5	1.883		
SE	.88	.63							
CV	13.11	11.20							
n	3	4							
Forearm length									
Mean	45.00	46.75			Sex	1	5.250	5.53	.066
SD	1.00	.96			Within	5	.950		
SE	.58	.48							
CV	2.22	2.05							
n	3	4							
Weight									
Mean	11.67	11.25			Sex	1	.298	1.05	.352
SD	.58	.50			Within	5	.283		
SE	.33	.25							
CV	4.97	4.44							
n	3	4							
Length of digit one									
Mean	8.67	8.75			Sex	1	.012	.02	.900
SD	.58	.96			Within	5	.683		
SE	.33	.48							
CV	6.69	10.97							
n	3	4							

Table 9.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	93.67	92.50			Sex	1	2.333	.13	.733
SD	6.03	2.38			Within	5	17.933		
SE	3.48	1.19							
CV	6.44	2.57							
n	3	4							
Length of digit four									
Mean	65.33	66.00			Sex	1	.762	.26	.632
SD	2.52	.82			Within	5	2.933		
SE	1.45	.41							
CV	3.86	1.24							
n	3	4							
Length of digit five									
Mean	62.33	65.00			Sex	1	12.191	1.87	.230
SD	3.06	2.16			Within	5	6.533		
SE	1.76	1.08							
CV	4.91	3.32							
n	3	4							
Tibia length									
Mean	21.00	21.50			Sex	1	.429	.71	.437
SD	1.00	.58			Within	5	.600		
SE	.58	.30							
CV	4.76	2.70							
n	3	4							
Calcar length									
Mean	19.67	21.00			Sex	1	3.048	.57	.484
SD	.58	2.94			Within	5	5.333		
SE	.33	1.47							
CV	2.95	14.00							
n	3	4							
Noseleaf length									
Mean	15.67	13.75			Sex	1	6.298	2.76	.158
SD	2.08	.96			Within	5	2.283		
SE	1.20	.48							
CV	13.27	6.98							
n	3	4							
Greatest length of skull									
Mean	19.93	20.10			Sex	1	.048	1.05	.352
SD	.21	.22			Within	5	.045		
SE	.12	.11							
CV	1.05	1.09							
n	3	4							
Condylobasal length									
Mean	17.53	18.10			Sex	1	.551	21.73	.006
SD	.25	0			Within	5	.025		
SE	.15	0							
CV	1.43	0							
n	3	4							
Zygomatic breadth									
Mean	11.53	11.45			Sex	1	.012	.20	.673
SD	.25	.24			Within	5	.059		
SE	.15	.12							
CV	2.17	2.10							
n	3	4							

Table 9.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Postorbital constriction					
Mean	4.00	3.90			Sex	1	.017	.48	.521
SD	.27	.12			Within	5	.036		
SE	.15	.06							
CV	6.75	3.08							
n	3	4							
				Mastoid breadth					
Mean	11.30	11.30			Sex	1	.000	0	1.000
SD	.20	.20			Within	5	.040		
SE	.12	.10							
CV	1.77	1.77							
n	3	4							
				Breadth of braincase					
Mean	7.97	7.98			Sex	1	.000	.00	.950
SD	.21	.13			Within	5	.027		
SE	.12	.06							
CV	2.63	1.63							
n	3	4							
				Rostral breadth					
Mean	5.03	4.88			Sex	1	.043	2.28	.191
SD	.15	.13			Within	5	.019		
SE	.09	.06							
CV	2.98	2.66							
n	3	4							
				Height of braincase					
Mean	11.07	10.90			Sex	1	.048	2.75	.158
SD	.12	.14			Within	5	.017		
SE	.07	.07							
CV	1.08	1.28							
n	3	4							
				Breadth across the upper molars					
Mean	8.13	7.93			Sex	1	.074	1.36	.297
SD	.31	.17			Within	5	.055		
SE	.18	.09							
CV	3.81	2.14							
n	3	4							
				Breadth across the upper canines					
Mean	4.97	4.78			Sex	1	.063	4.25	.094
SD	.15	.10			Within	5	.015		
SE	.09	.05							
CV	3.02	2.09							
n	3	4							
				Length of the maxillary toothrow					
Mean	7.13	7.15			Sex	1	.000	.14	.721
SD	.06	.06			Within	5	.003		
SE	.03	.03							
CV	.84	.84							
n	3	4							
				Length of the upper molariform toothrow					
Mean	5.73	5.83			Sex	1	.014	.76	.422
SD	.21	.05			Within	5	.019		
SE	.12	.03							
CV	3.66	.86							
n	3	4							

Table 9.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Width of the widest molar									
Mean	2.23	2.33			Sex	1	.014	2.11	.206
SD	.06	.10			Within	5	.007		
SE	.03	.05							
CV	2.69	4.29							
n	3	4							
Greatest length of the mandible									
Mean	12.83	13.03			Sex	1	.063	1.24	.316
SD	.29	.17			Within	5	.051		
SE	.17	.09							
CV	2.26	1.30							
n	3	4							
Length of the mandibular toothrow									
Mean	7.93	7.68			Sex	1	.114	6.07	.057
SD	.15	.13			Within	5	.019		
SE	.09	.06							
CV	1.89	1.69							
n	3	4							
Length of the coronoid process									
Mean	4.13	4.18			Sex	1	.003	.06	.811
SD	.25	.19			Within	5	.047		
SE	.15	.10							
CV	6.05	4.55							
n	3	4							

(1973), and Taddei (1975*a*) considered Brazilian specimens in their work.

Valdez (1970) was unable to detect statistically significant secondary sexual variation in specimens of *P. discolor* utilizing univariate procedures on a number of morphometric characters. A multivariate analysis of variance on samples drawn from throughout the range of *P. discolor* has indicated strong sexual dimorphism while the subsequent use of discriminant function analysis indicated that mastoid breadth and to a lesser extent zygomatic breadth are important characters in distinguishing between the sexes (Power and Tamsitt, 1973). These authors cautioned, however, that the differences between males and females are not simply explained by size differentials but rather include subtle considerations of shape not detectable by univariate methods alone.

In samples restricted to southwestern São Paulo, Taddei (1975*a*) found males larger on the average than females for 17 external characters and 15 cranial characters. Statistically significant secondary sexual variation was found in breadth across the canines, breadth across the molars, zygomatic width, mastoid breadth, cranial depth, ear length, length of the second phalanx in digit III and length of the second phalanx in digit V. Strong sexual dimorphism is indicated by these results with males consistently larger than females.

The results of univariate analysis of 30 external and cranial characters on specimens from the Northeast of Brazil are shown in Table 10. Statistically significant geographic variation is observed in two cranial and two external characters (hindfoot length, length of digit IV, breadth of braincase, and length of the coronoid process). A consistent pattern for mean values is not evident–Caatingas populations have larger sample means than Cerrado populations for six characters, yet Cerrado populations have larger sample means than Caatingas populations for seven characters. In contrast, strong sexual dimorphism is evident. Males have larger sample means than females for eight external and eight cranial characters. Two external and nine cranial characters (forearm length, length of digit one, greatest length of skull, condylobasal length, mastoid breadth, breadth across the braincase, breadth across the upper molars, length of the maxillary tooth row, length

Table 10.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Phyllostomus discolor *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean	96.30	98.31	98.50	98.70	Area	1	25.505	2.28	.136
SD	4.08	3.14	3.58	2.83	Sex	1	18.648	1.67	.201
SE	1.29	.78	.80	.63	A × S	1	12.515	1.12	.294
CV	4.24	3.19	3.63	2.87	Error	62	11.173		
n	10	16	20	20					
				Tail length					
Mean	14.90	15.13	14.65	14.05	Area	1	7.736	3.91	.052
SD	1.66	1.31	1.47	1.28	Sex	1	.288	.15	.704
SE	.53	.33	.33	.29	A × S	1	2.002	1.01	.318
CV	11.14	18.66	10.10	9.11	Error	62	1.977		
n	10	16	20	20					
				Hindfoot length					
Mean	13.20	13.19	13.70	13.45	Area	1	2.215	4.14	.046
SD	.79	.66	.73	.76	Sex	1	.263	.49	.486
SE	.25	.16	.16	.17	A × S	1	.215	.40	.529
CV	5.98	5.00	5.33	5.65	Error	62	.535		
n	10	16	20	20					
				Ear length					
Mean	21.60	21.13	20.80	21.80	Area	1	.060	.03	.863
SD	1.35	1.15	1.15	1.80	Sex	1	1.050	.53	.469
SE	.43	.29	.26	.40	A × S	1	8.288	4.19	.045
CV	6.25	5.44	5.53	8.26	Error	62	1.977		
n	10	16	20	20					
				Tragus length					
Mean	8.90	8.81	9.05	9.00	Area	1	.434	.78	.379
SD	.74	.91	.61	.73	Sex	1	.072	.13	.719
SE	.23	.23	.14	.16	A × S	1	.005	.01	.922
CV	8.31	10.33	6.74	8.11	Error	62	.553		
n	10	16	20	20					
				Forearm length					
Mean	61.60	59.81	60.20	59.70	Area	1	8.715	3.14	.081
SD	1.84	1.52	1.80	1.56	Sex	1	19.934	7.18	.009
SE	.59	.38	.40	.35	A × S	1	6.315	2.27	.137
CV	2.99	2.54	2.99	2.61	Error	62	2.778		
n	10	16	20	20					
				Weight					
Mean	37.50	40.06	38.85	36.68	Area	1	15.815	1.49	.227
SD	3.27	3.29	2.16	4.05	Sex	1	.572	.05	.817
SE	1.03	.82	.48	.91	A × S	1	85.501	8.05	.006
CV	8.72	8.21	5.56	11.04	Error	62	10.615		
n	10	16	20	20					
				Length of digit one					
Mean	11.30	11.13	11.75	11.35	Area	1	1.736	4.46	.039
SD	.48	.50	.64	.75	Sex	1	1.260	3.23	.077
SE	.15	.13	.14	.17	A × S	1	.193	.50	.484
CV	4.25	4.49	5.45	6.61	Error	62	.390		
n	10	16	20	20					

Table 10.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of digit three					
Mean	109.10	105.00	105.55	105.50	Area	1	35.438	3.33	.073
SD	3.60	2.68	2.46	4.10	Sex	1	65.610	6.17	.016
SE	1.14	.67	.55	.92	A × S	1	62.486	5.88	.018
CV	3.30	2.55	2.33	3.89	Error	62	10.627		
n	10	16	20	20					
				Length of digit four					
Mean	80.70	78.31	78.65	78.15	Area	1	18.648	2.50	.119
SD	2.83	1.89	2.06	3.68	Sex	1	31.763	4.26	.043
SE	.90	.47	.46	.82	A × S	1	13.572	1.82	.182
CV	3.51	2.41	2.62	4.71	Error	62	7.462		
n	10	16	20	20					
				Length of digit five					
Mean	73.40	71.63	71.85	71.35	Area	1	12.688	2.28	.136
SD	2.01	2.06	1.98	3.00	Sex	1	19.717	3.54	.065
SE	.64	.52	.44	.67	A × S	1	6.193	1.11	.296
CV	2.74	2.88	2.76	4.20	Error	62	5.569		
n	10	16	20	20					
				Tibia length					
Mean	24.70	24.88	25.45	24.45	Area	1	.402	.26	.615
SD	1.83	.89	1.32	1.10	Sex	1	2.593	1.64	.205
SE	.58	.22	.29	.25	A × S	1	5.260	3.34	.073
CV	7.41	3.58	5.19	4.50	Error	62	1.577		
n	10	16	20	20					
				Calcar length					
Mean	9.80	9.75	9.55	10.05	Area	1	.010	.01	.917
SD	.92	1.13	.95	.76	Sex	1	.771	.88	.353
SE	.29	.28	.21	.17	A × S	1	1.152	1.31	.257
CV	9.38	11.59	9.95	7.56	Error	62	.879		
n	10	16	20	20					
				Noseleaf length					
Mean	6.70	6.19	6.50	6.40	Area	1	.001	.00	.972
SD	.48	.91	.51	.75	Sex	1	1.429	2.92	.092
SE	.15	.23	.12	.17	A × S	1	.648	1.32	.254
CV	7.16	14.70	7.85	11.72	Error	62	.489		
n	10	16	20	20					
				Greatest length of skull					
Mean	29.22	29.18	29.44	28.65	Area	1	.345	1.06	.307
SD	.52	.61	.65	.47	Sex	1	2.562	7.87	.007
SE	.17	.15	.15	.11	A × S	1	2.016	6.19	.016
CV	1.78	2.09	2.21	1.64	Error	61	.326		
n	9	16	20	20					
				Condylobasal length					
Mean	26.34	26.22	26.61	25.71	Area	1	.234	.80	.375
SD	.62	.51	.48	.58	Sex	1	3.845	13.10	.001
SE	.21	.13	.11	.13	A × S	1	2.191	7.47	.008
CV	2.35	1.95	1.80	2.26	Error	61	.294		
n	9	16	20	20					
				Zygomatic breadth					
Mean	15.23	15.56	15.55	14.94	Area	1	.342	2.07	.156
SD	.46	.37	.39	.43	Sex	1	.288	1.74	.192
SE	.15	.09	.09	.10	A × S	1	3.224	19.48	<.001
CV	3.02	2.38	2.51	2.88	Error	61	.166		
n	9	16	20	20					

Table 10.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Postorbital constriction				
Mean	6.47	6.38	6.38	6.37	Area	1	.035	.63	.432
SD	.15	.16	.26	.28	Sex	1	.033	.59	.444
SE	.05	.04	.06	.06	A × S	1	.021	.37	.545
CV	2.32	2.51	4.08	4.40	Error	61	.056		
n	9	16	20	20					
					Mastoid breadth				
Mean	14.42	14.78	14.91	14.19	Area	1	.042	.38	.538
SD	.24	.38	.37	.32	Sex	1	.493	4.50	.038
SE	.08	.08	.08	.07	A × S	1	4.207	38.41	<.001
CV	1.66	2.23	2.48	2.26	Error	61	.110		
n	9	16	20	20					
					Breadth of braincase				
Mean	12.13	12.03	12.04	11.82	Area	1	.339	5.10	.028
SD	.20	.18	.30	.29	Sex	1	.379	5.70	.020
SE	.07	.04	.07	.07	A × S	1	.051	.76	.385
CV	1.65	1.50	2.49	2.45	Error	61	.067		
n	9	16	20	20					
					Rostral breadth				
Mean	6.74	6.96	7.07	6.67	Area	1	.003	.06	.815
SD	.29	.19	.23	.25	Sex	1	.129	2.27	.137
SE	.10	.05	.05	.06	A × S	1	.368	24.03	<.001
CV	4.30	2.73	3.25	3.75	Error	61	.057		
n	9	16	20	20					
					Height of braincase				
Mean	13.18	13.33	13.33	12.99	Area	1	.122	.94	.336
SD	.43	.27	.30	.44	Sex	1	.136	1.05	.311
SE	.14	.07	.07	.10	A × S	1	.868	6.68	.012
CV	3.26	2.03	2.25	3.39	Error	61	.130		
n	9	16	20	20					
					Breadth across the upper molars				
Mean	9.86	9.76	9.98	9.73	Area	1	.028	.32	.573
SD	.24	.32	.25	.34	Sex	1	.446	5.04	.028
SE	.08	.08	.06	.08	A × S	1	.083	.94	.337
CV	2.43	3.29	2.51	3.49	Error	61	.089		
n	9	16	20	20					
					Breadth across the upper canines				
Mean	6.88	7.21	7.27	6.75	Area	1	.018	.42	.518
SD	.15	.22	.21	.22	Sex	1	.126	2.94	.092
SE	.05	.05	.05	.05	A × S	1	2.670	62.52	<.001
CV	2.18	3.05	2.89	3.26	Error	61	.043		
n	9	16	20	20					
					Length of the maxillary toothrow				
Mean	9.53	9.53	9.69	9.37	Area	1	.000	.01	.922
SD	.19	.18	.15	.22	Sex	1	.391	11.16	.001
SE	.06	.04	.03	.05	A × S	1	.381	10.87	002
CV	1.99	1.89	1.55	2.35	Error	61	.035		
n	9	16	20	20					
					Length of the upper molariform toothrow				
Mean	7.59	7.43	7.60	7.47	Area	1	.009	.24	.624
SD	.16	.23	.17	.20	Sex	1	.302	8.07	.006
SE	.05	.06	.04	.04	A × S	1	.003	.07	.786
CV	2.11	3.10	2.24	2.68	Error	61	.038		
n	9	16	20	20					

Table 10.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Width of the widest molar				
Mean	2.12	2.06	2.13	2.08	Area	1	.001	.08	.781
SD	.11	.14	.09	.08	Sex	1	.044	4.02	.050
SE	.04	.04	.02	.02	A × S	1	.000	.03	.860
CV	5.19	6.80	4.23	3.85	Error	61	.011		
n	9	16	20	20					
					Greatest length of the mandible				
Mean	19.31	19.30	19.43	18.76	Area	1	.648	3.82	.055
SD	.38	.39	.40	.45	Sex	1	1.696	9.98	.003
SE	.13	.10	.09	.10	A × S	1	1.587	9.34	.003
CV	1.97	2.02	2.06	2.40	Error	61	.170		
n	9	16	20	20					
					Length of the mandibular toothrow				
Mean	10.34	10.59	10.75	10.39	Area	1	.142	1.98	.165
SD	.27	.29	.31	.19	Sex	1	.049	.68	.412
SE	.09	.07	.07	.04	A × S	1	1.379	19.27	<.001
CV	2.61	2.74	2.88	1.83	Error	61	.072		
n	9	16	20	20					
					Length of the coronoid process				
Mean	6.38	6.74	7.03	6.79	Area	1	1.789	16.44	<.001
SD	.29	.29	.34	.37	Sex	1	.048	.44	.509
SE	.10	.07	.08	.08	A × S	1	1.337	12.28	<.001
CV	4.55	4.30	4.84	5.45	Error	61	.109		
n	9	16	20	20					

of the upper molariform tooth row, width of the widest molar, and greatest length of the maxilla) exhibit statistically significant secondary sexual variation. In the only case where females have a larger sample mean values than males (total length), statistical significance is not observed.

Clearly, when samples are from a restricted locality, as in the work of Taddei (1975*a*) or when geographic differences between sampling localities can be statistically controlled, as in the analyses for the Caatingas and Cerrado, strong sexual dimorphism has been detected by univariate analyses with males consistently larger than females. Perhaps the inclusion of specimens from disparate localities has confounded the results in the work of Valdez (1970). Similarly, the large morphometric heterogeneity attributable to geographic differences in the samples used by Power and Tamsitt (1973) may have prevented a simple set of unipolar size vectors from accounting for the differences between the sexes shown by discriminant function analysis.

Phyllostomus hastatus (Pallas, 1767)

P. h. hastatus is the presently recognized subspecies designation for populations of this species in the Northeast of Brazil (Jones and Carter, 1976). This large omnivore was rare in the Caatingas but widespread and common in both Cerrado and Cerradão habitats on the Chapada do Araripe. A colony of more than 100 individuals roosted in a small attic-like space (6 m by .5 m by .5 m) in the entrance arch to the Colégio Agrícola de Crato; the roost was also occupied by a larger colony of *Molossus molossus* (>300 individuals). Of the 108 individuals of *P. h. hastatus* eventually captured from the roost, 48 were males. This strongly suggests an equal sex ratio (Binomial Test, $P > .05$) and the absence of harem groups within the colony (contrary to the situation reported by Bradbury, 1977).

Swanepoel and Genoways (1979) cite authors who have published morphometric data on *P. hastatus.* G. M. Allen (1908), Lima (1926), Cunha Vieira (1942), and Taddei (1975*a*) are the only workers who have included Brazilian specimens in their accounts. The work of Taddei (1975*a*) is unique because he performed statistical analyses on large samples. He detected statistically significant secondary sexual variation in all 17 of the cranial characters examined and for eight of the 17 external characters. Males are larger on the average than females in all cases. The results from the Northeast of Brazil are comparable (Table 11). Males have larger sample means than females for all but two of the 30 variables. Statistically significant secondary sexual variation is detected in 15 of the 16 cranial characters and in eight of the 14 external characters. Clearly, *P. hastatus* is dimorphic with males larger than females.

Trachops cirrhosus (Spix, 1823)

Of the three nominal subspecies currently in use, *T. c. cirrhosus* is the appellation appropriate for Northeast Brazilian populations of this omnivore because its type locality is in Pernambuco (Jones and Carter, 1976). The distribution of *T. c. cirrhosus* in the Caatingas was restricted to serrotes or areas containing rock outcroppings and it was absent from both Cerrado and Cerradão habitats on the Chapada do Araripe. Sixteen of 35 individuals captured from the Caatingas were males, hence the sex ratio appears to be equal (Binomial Test, $P > .05$).

Peters (1865), Lima (1926), Cunha Vieira (1942), and Felten (1956) are the only authors among the group cited by Swanepoel and Genoways (1979) to include measurements of *T. cirrhosus* from Brazil. Information concerning individual variation is conspicuously absent from the literature and secondary sexual variation has not been examined in this species. The results of a statistical analysis of individual and secondary sexual variation for *T. c. cirrhosus* are given in Table 12. Only a single character exhibits statistically significant secondary sexual variation (breadth across the upper canines). Males have larger sample means than females for all of the cranial characters and four of the external characters while females have larger sample means than males for 10 external characters. Because of the relatively large sample sizes, low levels of significance associated with the analyses of variance and minor differences encountered between male and female mean values, it seems prudent to suggest that *T. cirrhosus* does not exhibit sexual dimorphism.

Subfamily Glossophaginae

Glossophaga soricina (Pallas, 1766)

This nectarivore was abundant and ubiquitous in Cerrado, Cerradão, and most habitats of the Caatingas; it is particularly dominant in disturbed or second growth areas. Abandoned man-made structures and caves were preferred roosting sites and colony size may exceed 2,000 individuals. Aggregations of *Carollia perspicillata* containing up to 20 individuals were frequently found roosting in association with *G. soricina* throughout the Northeast. Small groups of bats were frequently observed foraging near fruiting plants. *Solanum psniculatum* was the predominant fruit in the diet of Caatingas specimens whereas the fruit of *Vismia* was preferred in the Cerrado (although *Solanum* was also consumed). Males and females occurred in statistically indistinguishable proportions in the Caatingas (Binomial Test, $P > .05$); 46% of the 421 captured adult specimens were males. On the Chapada do Araripe, 56% of the 494 captured adult specimens were males. Although the proportion of males and females did differ significantly (Binomial Test, $P < .01$), the magnitude of the difference was small and probably reflects the vagaries of sampling by mist net rather than characteristics of the social structure in this species.

In the Caatingas, some sexual segregation occurred within the large roosts that occurred in abandoned buildings. Females tended to congregate as a central unit; males occupied more dispersed solitary locations at the periphery of the roost. This phenomenon became particularly evident as the time of parturition approached.

Of the four generally recognized subspecies, *Glossophaga s. soricina* is the designation applied to Brazilian specimens (Jones and Carter, 1976). Many authors report morphometric data on *G. soricina* (see Swanepoel and Genoways, 1979), but only Miller (1913), Lima (1926), Cunha Vieira (1942), and Taddei (1975*b*) include specimens from Brazil. Taddei (1975*b*) is unique among these authors in working with large samples of *G. soricina* and performing statistical analyses on numerous morphometric characters. He finds statistically significant sexual dimorphism in four of 17 external characters (head-body length, forearm length, length of the fifth metacarpal and length of the fourth metacarpal); in all four cases males were larger, on the average, than females. Among the 15 cranial characters analyzed, statistically significant secondary sexual variation is apparent in seven characters (length of molar, mandibular toothrow length, breadth across the canines, zygomatic breadth, braincase breadth, mastoid breadth, and depth of the cranium); females are larger on the average for the first two characters while males are larger on the average for the latter five characters.

The results of statistical analyses on the specimens of *G. s. soricina* from the Northeast of Brazil are

Table 11.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Phyllostomus hastatus *males and females from both the Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (P < 0.50) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean	123.00	119.43	127.25	119.75	Sex	1	643.527	34.46	<.001
SD	—	1.81	4.19	5.07	Within	46	18.673		
SE	—	.69	.94	1.13					
CV	—	1.52	3.29	4.23					
n	1	7	20	20					
				Tail length					
Mean	19.00	17.86	19.15	18.50	Sex	1	7.741	1.60	.212
SD	—	2.04	1.93	2.57	Within	46	4.839		
SE	—	.77	.43	.57					
CV	—	11.42	10.08	13.89					
n	1	7	20	20					
				Hindfoot length					
Mean	17.00	17.57	17.75	17.05	Sex	1	3.307	2.80	.101
SD	—	.98	1.07	1.15	Within	46	1.182		
SE	—	.37	.24	.26					
CV	—	5.58	6.03	6.74					
n	1	7	20	20					
				Ear length					
Mean	28.00	28.14	28.90	27.75	Sex	1	11.938	7.23	.010
SD	—	1.57	.97	1.48	Within	46	1.652		
SE	—	.60	.22	.33					
CV	—	5.58	3.36	5.33					
n	1	7	20	20					
				Tragus length					
Mean	13.00	13.08	13.20	13.20	Sex	1	.021	.06	.810
SD	—	.58	.62	.62	Within	46	.062		
SE	—	.22	.14	.14					
CV	—	4.46	4.70	4.70					
n	1	7	20	20					
				Forearm length					
Mean	81.00	81.29	84.30	81.55	Sex	1	83.667	20.33	<.001
SD	—	2.50	1.63	2.19	Within	46	4.116		
SE	—	.94	.36	.49					
CV	—	3.08	1.93	2.69					
n	1	7	20	20					
				Weight					
Mean	94.50	84.64	93.43	81.68	Sex	1	1,437.574	21.46	<.001
SD	—	8.94	8.58	7.80	Within	46	66.987		
SE	—	3.38	1.92	1.74					
CV	—	10.56	9.18	9.55					
n	1	7	20	20					
				Length of digit one					
Mean	13.00	14.14	14.05	14.25	Sex	1	.583	.55	.462
SD	—	1.07	1.28	.72	Within	46	1.058		
SE	—	.40	.29	.16					
CV	—	7.57	9.11	5.05					
n	1	7	20	20					

Table 11.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	145.00	145.86	147.35	143.95	Sex	1	92.191	5.64	.022
SD	—	3.80	3.42	4.86	Within	46	16.358		
SE	—	1.16	.77	1.09					
CV	—	2.11	2.32	3.38					
n	1	7	20	20					
Length of digit four									
Mean	108.00	108.00	110.70	107.85	Sex	1	85.003	5.60	.022
SD	—	1.83	3.91	4.48	Within	46	15.170		
SE	—	.69	.87	1.00					
CV	—	1.69	3.53	4.15					
n	1	7	20	20					
Length of digit five									
Mean	98.00	99.14	102.15	98.15	Sex	1	148.446	14.42	<.001
SD	—	1.68	3.20	3.65	Within	46	10.293		
SE	—	.63	.69	.82					
CV	—	1.69	3.03	3.72					
n	1	7	20	20					
Tibia length									
Mean	32.00	32.57	33.65	32.75	Sex	1	8.894	10.03	.003
SD	—	.54	.67	1.21	Within	46	.886		
SE	—	.20	.15	.27					
CV	—	1.66	1.99	3.69					
n	1	7	20	20					
Calcar length									
Mean	19.00	21.29	21.35	20.40	Sex	1	4.373	1.93	.171
SD	—	1.11	1.66	1.35	Within	46	2.263		
SE	—	.42	.37	.30					
CV	—	5.21	7.78	6.62					
n	1	7	20	20					
Noseleaf length									
Mean	9.00	9.14	8.95	9.30	Sex	1	1.112	3.62	.063
SD	—	.38	.39	.73	Within	46	.307		
SE	—	.14	.09	.16					
CV	—	4.16	4.36	7.85					
n	1	7	20	20					
Greatest length of skull									
Mean	36.20	35.04	36.93	35.29	Sex	1	32.917	63.35	<.001
SD	—	.26	.96	.51	Within	46	.520		
SE	—	.10	.21	.12					
CV	—	.74	2.60	1.45					
n	1	7	20	20					
Condylobasal length									
Mean	32.20	31.16	32.70	31.16	Sex	1	27.011	92.12	<.001
SD	—	.38	.65	.48	Within	46	.293		
SE	—	.14	.15	.11					
CV	—	1.22	1.99	1.54					
n	1	7	20	20					
Zygomatic breadth									
Mean	20.90	19.54	20.93	19.70	Sex	1	19.000	68.79	<.001
SD	—	.47	.67	.39	Within	46	.276		
SE	—	.18	.15	.09					
CV	—	2.41	3.20	1.98					
n	1	7	20	20					

Table 11.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	6.80	6.66	7.03	6.83	Sex	1	.620	15.01	<.001
SD	—	.19	.23	.16	Within	46	.041		
SE	—	.07	.05	.04					
CV	—	2.85	3.27	2.34					
n	1	7	20	20					
Mastoid breadth									
Mean	19.30	18.14	19.46	18.00	Sex	1	23.627	145.84	<.001
SD	—	.28	.51	.32	Within	46	.162		
SE	—	.10	.11	.07					
CV	—	1.54	2.62	1.78					
n	1	7	20	20					
Breadth of braincase									
Mean	14.00	13.59	14.04	13.63	Sex	1	2.080	28.22	<.001
SD	—	.11	.29	.30	Within	46	.074		
SE	—	.04	.07	.07					
CV	—	.81	2.07	2.20					
n	1	7	20	20					
Rostral breadth									
Mean	9.50	9.09	9.65	9.14	Sex	1	3.099	56.09	<.001
SD	—	.23	.25	.24	Within	46	.055		
SE	—	.09	.06	.05					
CV	—	2.53	2.59	2.63					
n	1	7	20	20					
Height of braincase									
Mean	16.70	16.11	17.11	16.15	Sex	1	10.631	48.38	<.001
SD	—	.27	.62	.34	Within	46	.220		
SE	—	.10	.14	.08					
CV	—	1.68	3.62	2.11					
n	1	7	20	20					
Breadth across the upper molars									
Mean	13.00	12.86	13.56	13.22	Sex	1	1.997	23.00	<.001
SD	—	.31	.24	.27	Within	46	.087		
SE	—	.12	.05	.06					
CV	—	2.41	1.77	2.04					
n	1	7	20	20					
Breadth across the upper canines									
Mean	9.30	8.67	9.75	9.01	Sex	1	7.590	121.03	<.001
SD	—	.18	.23	.21	Within	46	.063		
SE	—	.07	.05	.05					
CV	—	2.08	2.36	2.33					
n	1	7	20	20					
Length of the maxillary toothrow									
Mean	13.10	12.70	13.33	12.81	Sex	1	3.414	54.65	<.001
SD	—	.33	.28	.19	Within	46	.063		
SE	—	.12	.06	.04					
CV	—	2.60	2.10	1.58					
n	1	7	20	20					
Length of the upper molariform toothrow									
Mean	10.20	9.83	10.09	9.91	Sex	1	.480	12.24	<.001
SD	—	.24	.21	.17	Within	46	.039		
SE	—	.09	.05	.04					
CV	—	2.44	2.08	1.72					
n	1	7	20	20					

Table 11.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Width of the widest molar									
Mean	3.30	3.41	3.43	3.32	Sex	1	.066	3.52	.067
SD	—	.19	.15	.10	Within	46	.019		
SE	—	.07	.03	.02					
CV	—	7.48	4.37	3.01					
n	1	7	20	20					
Greatest length of the mandible									
Mean	24.90	24.11	25.50	24.16	Sex	1	20.801	90.70	<.001
SD	—	.27	.55	.46	Within	46	.229		
SE	—	.10	.12	.10					
CV	—	1.12	2.16	1.90					
n	1	7	20	20					
Length of the mandibular toothrow									
Mean	14.80	14.14	15.23	14.47	Sex	1	8.027	84.45	<.001
SD	—	.35	.30	.26	Within	46	.095		
SE	—	.13	.07	.06					
CV	—	2.48	1.96	1.80					
n	1	7	20	20					
Length of the coronoid process									
Mean	10.70	9.86	11.13	10.31	Sex	1	9.932	68.63	<.001
SD	—	.26	.44	.27	Within	46	.145		
SE	—	.10	.10	.06					
CV	—	2.64	3.95	2.62					
n	1	7	20	20					

Table 12.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Trachops cirrhosus *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	100.81	98.58			Sex	1	43.331	.70	.409
SD	7.63	8.07			Within	33	61.972		
SE	1.91	1.85							
CV	7.57	8.19							
n	16	19							
Tail length									
Mean	15.75	15.63			Sex	1	.122	.03	.875
SD	2.32	2.09			Within	33	4.831		
SE	.58	.48							
CV	14.73	13.37							
n	16	19							
Hindfoot length									
Mean	16.25	16.26			Sex	1	.002	.00	.963
SD	.68	.93			Within	33	.687		
SE	.17	.21							
CV	4.18	5.72							
n	16	19							

Table 12.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Ear length									
Mean	32.31	33.58			Sex	1	.617	.17	.681
SD	2.02	1.77			Within	33	3.578		
SE	.51	.41							
CV	6.25	5.27							
n	16	19							
Tragus length									
Mean	13.31	13.58			Sex	1	.617	.72	.401
SD	.95	.90			Within	33	.851		
SE	.24	.21							
CV	7.14	6.63							
n	16	19							
Forearm length									
Mean	60.94	61.21			Sex	1	.648	.27	.604
SD	1.29	1.72			Within	33	2.367		
SE	.32	.39							
CV	2.12	2.81							
n	16	19							
Weight									
Mean	38.88	39.16			Sex	1	.695	.02	.898
SD	4.46	7.68			Within	33	41.221		
SE	1.12	1.76							
CV	11.47	19.61							
n	16	19							
Length of digit one									
Mean	14.19	14.95			Sex	1	.001	.00	.975
SD	.77	1.03			Within	33	.845		
SE	.19	.24							
CV	5.15	6.89							
n	16	19							
Length of digit three									
Mean	115.50	115.58			Sex	1	.054	.00	.951
SD	3.16	4.18			Within	33	14.080		
SE	.79	.96							
CV	2.74	3.62							
n	16	19							
Length of digit four									
Mean	85.06	85.68			Sex	1	3.357	.44	.511
SD	2.57	2.91			Within	33	7.607		
SE	.64	.67							
CV	3.02	3.40							
n	16	19							
Length of digit five									
Mean	86.13	87.00			Sex	1	6.650	.78	.382
SD	2.75	3.04			Within	33	8.477		
SE	.69	.70							
CV	3.19	3.49							
n	16	19							
Tibia length									
Mean	28.13	28.00			Sex	1	.136	.05	.821
SD	.81	2.06			Within	33	2.599		
SE	.20	.47							
CV	2.88	7.36							
n	16	19							

Table 12.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Calcar length				
Mean	13.81	13.95			Sex	1	.158	.11	.742
SD	.91	1.39			Within	33	1.436		
SE	.23	.32							
CV	6.59	9.96							
n	16	19							
					Noseleaf length				
Mean	8.25	8.00			Sex	1	.543	.94	.339
SD	.68	.82			Within	33	.576		
SE	.17	.19							
CV	8.24	10.25							
n	16	19							
					Greatest length of skull				
Mean	28.11	27.94			Sex	1	.261	.14	.715
SD	.69	.73			Within	32	.506		
SE	.18	.17							
CV	2.45	2.61							
n	15	19							
					Condylobasal length				
Mean	25.05	24.78			Sex	1	.631	2.14	.153
SD	.51	.57			Within	32	.295		
SE	.13	.13							
CV	2.04	2.30							
n	15	19							
					Zygomatic breadth				
Mean	14.46	14.34			Sex	1	.117	.41	.525
SD	.52	.53			Within	32	.283		
SE	.14	.12							
CV	3.66	3.70							
n	15	19							
					Postorbital constriction				
Mean	13.79	13.63			Sex	1	.202	1.73	.198
SD	.29	.38			Within	32	.117		
SE	.07	.09							
CV	2.10	2.79							
n	15	19							
					Mastoid breadth				
Mean	5.29	5.28			Sex	1	.000	.00	.968
SD	.13	.21			Within	32	.031		
SE	.03	.05							
CV	2.46	3.98							
n	15	19							
					Breadth of braincase				
Mean	11.77	11.63			Sex	1	.165	2.80	.104
SD	.27	.22			Within	32	.059		
SE	.07	.05							
CV	2.29	1.89							
n	15	19							
					Rostral breadth				
Mean	6.16	6.03			Sex	1	.138	2.88	.100
SD	.26	.18			Within	32	.048		
SE	.07	.04							
CV	4.22	2.99							
n	15	19							

Table 12.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Height of braincase									
Mean	14.73	14.61			Sex	1	.113	.72	.403
SD	.45	.35			Within	32	.157		
SE	.12	.08							
CV	3.05	2.40							
n	15	19							
Breadth across the upper molars									
Mean	10.37	10.30			Sex	1	.045	.41	.525
SD	.39	.28			Within	32	.109		
SE	.10	.06							
CV	3.76	2.72							
n	15	19							
Breadth across the upper canines									
Mean	6.18	6.07			Sex	1	.095	5.45	.026
SD	.12	.14			Within	31	.017		
SE	.03	.03							
CV	1.94	2.31							
n	15	18							
Length of the maxillary toothrow									
Mean	10.35	10.27			Sex	1	.062	1.04	.316
SD	.28	.21			Within	31	.059		
SE	.07	.05							
CV	2.71	2.04							
n	15	18							
Length of the upper molariform toothrow									
Mean	8.30	8.30			Sex	1	.000	.01	.943
SD	.27	.16			Within	32	.045		
SE	.07	.04							
CV	3.25	1.93							
n	15	19							
Width of the widest molar									
Mean	3.16	3.10			Sex	1	.030	1.87	.181
SD	.14	.12			Within	32	.016		
SE	.04	.03							
CV	4.43	3.87							
n	15	19							
Greatest length of the mandible									
Mean	18.90	18.63			Sex	1	.628	3.63	.066
SD	.42	.41			Within	32	.173		
SE	.11	.09							
CV	2.22	2.20							
n	15	19							
Length of the mandibular toothrow									
Mean	11.29	11.14			Sex	1	.188	3.07	.089
SD	.31	.18			Within	32	.061		
SE	.08	.04							
CV	2.75	1.62							
n	15	19							
Length of the coronoid process									
Mean	5.48	5.46			Sex	1	.002	.02	.877
SD	.34	.29			Within	32	.098		
SE	.09	.07							
CV	6.20	5.31							
n	15	19							

Table 13.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Glossophaga soricina *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	63.90	63.90	63.30	64.75	Area	1	.313	.04	.837
SD	2.02	2.97	2.30	3.35	Sex	1	10.513	1.43	.236
SE	.45	.67	.51	.75	A × S	1	10.513	1.43	.236
CV	3.16	4.65	3.63	5.17	Error	76	7.363		
n	20	20	20	20					
Tail length									
Mean	8.95	9.20	8.05	9.05	Area	1	5.513	3.67	.059
SD	1.10	1.20	1.28	1.32	Sex	1	7.813	5.21	.025
SE	.25	.26	.29	.29	A × S	1	2.813	1.87	.175
CV	12.29	13.04	15.90	14.59	Error	76	1.501		
n	20	20	20	20					
Hindfoot length									
Mean	9.10	9.05	9.30	9.30	Area	1	1.013	2.83	.096
SD	.79	.39	.57	.57	Sex	1	.013	.03	.852
SE	.18	.09	.12	.12	A × S	1	.013	.03	.852
CV	8.68	4.31	6.13	6.13	Error	76	.357		
n	20	20	20	20					
Ear length									
Mean	13.10	13.30	13.25	13.35	Area	1	.200	.26	.611
SD	1.25	.57	.72	.81	Sex	1	.450	.59	.446
SE	.28	.13	.16	.18	A × S	1	.050	.07	.799
CV	9.54	4.29	5.43	6.07	Error	76	.767		
n	20	20	20	20					
Tragus length									
Mean	5.95	6.00	5.70	5.80	Area	1	1.013	2.71	.104
SD	.61	.46	.47	.83	Sex	1	.113	.30	.585
SE	.14	.10	.11	.19	A × S	1	.013	.03	.855
CV	10.25	7.67	8.25	14.31	Error	76	.373		
n	20	20	20	20					
Forearm length									
Mean	35.15	36.10	35.05	35.75	Area	1	1.103	1.35	.249
SD	.88	.97	.83	.79	Sex	1	13.613	18.13	<.001
SE	.20	.22	.19	.18	A × S	1	.313	.42	.521
CV	2.50	2.69	2.37	2.21	Error	76	.751		
n	20	20	20	20					
Weight									
Mean	9.40	10.50	10.18	10.63	Area	1	4.050	2.59	.112
SD	.45	1.48	.86	1.77	Sex	1	12.013	7.68	.007
SE	.10	.33	.19	.40	A × S	1	2.113	1.35	.249
CV	4.79	14.10	8.45	16.65	Error	76	1.564		
n	20	20	20	20					
Length of digit one									
Mean	7.95	7.95	7.90	8.05	Area	1	.013	.04	.851
SD	.69	.69	.55	.39	Sex	1	.113	.32	.573
SE	.15	.15	.12	.09	A × S	1	.113	.32	.573
CV	8.68	8.68	6.96	4.84	Error	76	.351		
n	20	20	20	20					

Table 13.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	68.55	69.40	69.00	69.70	Area	1	2.813	.72	.398
SD	1.91	2.31	1.69	2.06	Sex	1	12.013	3.08	.083
SE	.43	.49	.38	.46	A × S	1	.113	.03	.866
CV	2.79	3.18	2.45	2.96	Error	76	3.894		
n	20	20	20	20					
Length of digit four									
Mean	50.70	51.75	50.30	51.20	Area	1	4.513	1.89	.173
SD	1.63	1.68	1.26	1.58	Sex	1	19.013	7.97	.006
SE	.36	.38	.28	.35	A × S	1	.113	.05	.829
CV	3.21	3.25	2.50	3.09	Error	76	2.386		
n	20	20	20	20					
Length of digit five									
Mean	48.15	48.85	47.30	48.75	Area	1	4.513	2.21	.141
SD	1.50	1.50	1.03	1.62	Sex	1	23.113	11.33	.001
SE	.34	.34	.23	.36	A × S	1	2.813	1.38	.244
CV	3.12	3.07	2.18	3.32	Error	76	2.040		
n	20	20	20	20					
Tibia length									
Mean	14.75	15.15	14.60	14.90	Area	1	.800	1.97	.165
SD	.79	.59	.60	.55	Sex	1	2.450	6.03	.016
SE	.18	.13	.13	.12	A × S	1	.050	.12	.727
CV	5.36	3.89	4.11	3.69	Error	76	.407		
n	20	20	20	20					
Calcar length									
Mean	5.00	4.95	4.70	5.05	Area	1	.200	.76	.387
SD	.32	.61	.47	.61	Sex	1	.450	1.70	.196
SE	.07	.14	.11	.14	A × S	1	.800	3.02	.086
CV	6.40	12.32	10.00	12.08	Error	76	.265		
n	20	20	20	20					
Noseleaf length									
Mean	4.05	4.10	3.80	4.00	Area	1	.613	3.34	.072
SD	.39	.55	.41	.32	Sex	1	.313	1.70	.196
SE	.09	.12	.09	.07	A × S	1	.113	.61	.436
CV	9.63	13.41	10.79	8.00	Error	76	.184		
n	20	20	20	20					
Greatest length of skull									
Mean	20.45	20.54	20.29	20.53	Area	1	.136	1.07	.303
SD	.39	.31	.35	.36	Sex	1	.528	4.17	.045
SE	.09	.07	.08	.08	A × S	1	.105	.83	.365
CV	1.91	1.51	1.72	1.75	Error	76	.127		
n	20	20	20	20					
Condylobasal length									
Mean	19.15	19.30	19.09	19.23	Area	1	.098	.85	.359
SD	.41	.26	.35	.32	Sex	1	.421	3.66	.060
SE	.09	.06	.08	.07	A × S	1	.001	.00	.948
CV	2.14	1.35	1.83	1.66	Error	76	.115		
n	20	20	20	20					
Zygomatic breadth									
Mean	9.17	9.17	9.22	9.20	Area	1	.032	.90	.346
SD	.15	.16	.20	.23	Sex	1	.002	.06	.813
SE	.03	.04	.05	.05	A × S	1	.002	.06	.813
CV	3.06	1.74	2.17	2.50	Error	76	.036		
n	20	20	20	20					

Table 13.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	4.58	4.60	4.63	4.69	Area	1	.078	2.72	.103
SD	.14	.15	.22	.15	Sex	1	.028	.98	.326
SE	.03	.03	.05	.03	A × S	1	.006	.21	.646
CV	3.06	3.26	4.75	3.20	Error	76	.029		
n	20	20	20	20					
Mastoid breadth									
Mean	8.77	8.90	8.81	8.91	Area	1	.008	.25	.622
SD	.15	.13	.22	.20	Sex	1	.265	8.10	.006
SE	.03	.03	.05	.05	A × S	1	.005	.14	.712
CV	1.71	1.46	2.50	2.24	Error	76	.033		
n	20	20	20	20					
Breadth of braincase									
Mean	8.64	8.64	8.56	8.72	Area	1	.000	.000	1.000
SD	.20	.23	.20	.24	Sex	1	.145	3.02	.086
SE	.04	.05	.05	.06	A × S	1	.128	2.68	.106
CV	2.31	2.66	2.34	2.75	Error	76	.048		
n	20	20	20	20					
Rostral breadth									
Mean	3.82	3.82	3.83	3.87	Area	1	.015	.42	.517
SD	.17	.14	.21	.23	Sex	1	.006	.17	.680
SE	.04	.03	.05	.05	A × S	1	.006	.17	.680
CV	4.45	3.36	5.48	5.94	Error	76	.036		
n	20	20	20	20					
Height of braincase									
Mean	9.28	9.11	9.16	9.17	Area	1	.021	.27	.607
SD	.34	.13	.22	.37	Sex	1	.136	1.72	.194
SE	.08	.03	.05	.08	A × S	1	.153	1.93	.169
CV	3.66	1.43	2.40	4.03	Error	76	.079		
n	20	20	20	20					
Breadth across the upper molars									
Mean	5.33	5.33	5.34	5.33	Area	1	.000	.01	.936
SD	.12	.13	.15	.15	Sex	1	.001	.06	.810
SE	.03	.03	.03	.03	A × S	1	.001	.06	.810
CV	2.25	2.44	2.81	2.81	Error	76	.019		
n	20	20	20	20					
Breadth across the upper canines									
Mean	3.96	3.87	3.93	3.94	Area	1	.004	.29	.591
SD	.11	.15	.10	.13	Sex	1	.032	2.07	.154
SE	.02	.03	.02	.03	A × S	1	.050	3.24	.076
CV	2.78	3.88	2.54	3.30	Error	76	.015		
n	20	20	20	20					
Length of the maxillary toothrow									
Mean	6.99	7.04	6.97	7.04	Area	1	.002	.09	.770
SD	.19	.15	.15	.12	Sex	1	.072	3.11	.082
SE	.04	.03	.03	.03	A × S	1	.005	.19	.660
CV	2.72	2.13	2.15	1.70	Error	76	.023		
n	20	20	20	20					
Length of the upper molariform toothrow									
Mean	5.34	5.23	5.26	5.25	Area	1	.013	.41	.523
SD	.21	.17	.16	.15	Sex	1	.072	2.38	.127
SE	.05	.04	.04	.03	A × S	1	.050	1.65	.203
CV	3.93	3.25	3.04	2.86	Error	76	.030		
n	20	20	20	20					

Table 13.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Width of the widest molar									
Mean	.97	.96	.97	.91	Area	1	.010	1.89	.173
SD	.07	.09	.06	.08	Sex	1	.028	5.26	.025
SE	.02	.02	.01	.02	A × S	1	.015	2.83	.097
CV	7.22	9.38	6.19	8.79	Error	76	.005		
n	20	20	20	20					
Greatest length of the mandible									
Mean	13.79	13.89	13.73	13.87	Area	1	.032	.27	.604
SD	.27	.48	.33	.26	Sex	1	.245	2.24	.139
SE	.06	.11	.07	.06	A × S	1	.008	.07	.795
CV	1.96	3.46	2.40	1.87	Error	76	.118		
n	20	20	20	20					
Length of the mandibular toothrow									
Mean	7.40	7.44	7.31	7.37	Area	1	.010	.32	.571
SD	.20	.26	.18	.13	Sex	1	.171	5.46	.022
SE	.04	.06	.04	.03	A × S	1	.001	.04	.850
CV	2.70	3.49	2.46	1.76	Error	76	.031		
n	20	20	20	20					
Length of the coronoid process									
Mean	3.73	3.63	3.75	3.66	Area	1	.010	.32	.571
SD	.11	.18	.21	.19	Sex	1	.171	5.46	.022
SE	.03	.04	.05	.04	A × S	1	.001	.04	.850
CV	2.95	4.96	5.60	5.19	Error	76	.031		
n	20	20	20	20					

indicated in Table 13. Significant geographic differences between Caatingas and Cerrado sites are not apparent for any of the 30 analyzed variables, and a trend in average values between the sites is not obvious. Significant secondary sexual variation is indicated for six external characters (tail length, forearm length, weight, length of digit IV, length of digit V, and tibia length) and six cranial characters (greatest length of skull, condylobasal length, mastoid breadth, width of the widest molar, length from the canine to the last molar in the ramus, and length of the coronoid process). The sample means for females are larger than those for males for nine external characters and seven cranial characters while the sample means for males are larger than those for females for only two characters. Sexual dimorphism is more pronounced in Northeast Brazilian populations of *G. soricina* than in those from southwestern São Paulo. Further, the trend found in the Northeast of female sample means being consistently larger than male sample means is contrary to the results obtained by Taddei (1975*b*).

Lonchophylla mordax Thomas, 1903

Jones and Carter (1976) consider *L. mordax* to be a monotypic species, however, they note that it may be conspecific with *L. concava* as suggested by Handley (1966). This nectarivore was common in Caatingas habitats, especially at sites near serrotes. Because 51% of the 72 captured specimens were males, the sex ratio must be considered equal (Binomial Test, $P > .05$). *L. mordax* was apparently absent from the Chapada do Araripe.

Very little has been published on the morphometrics of *L. mordax* (see Swanepoel and Genoways, 1979) and nothing is known concerning individual variation or secondary sexual variation in this species. A statistical analysis of morphometric variation in a Caatingas population of *L. mordax* is presented in Table 14. Five external and four cranial characters exhibit statistically significant secondary sexual variation. It appears that secondary sexual variation in this species is related to skull shape rather than skull size and to the overall size of the wings, with females having larger wings than males on the average.

Anoura geoffroyi Gray, 1838

Three nominal subspecies of this nectarivore are recognized, with *A. g. geoffroyi* being the designation applied to Brazilian specimens (Jones and Carter, 1976). *A. g. geoffroyi* was uncommon in the

Table 14.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Lonchophylla mordax *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	64.81	66.14			Sex	1	31.914	2.86	.095
SD	3.47	3.19			Within	70	11.142		
SE	.57	.54							
CV	5.35	4.82							
n	37	35							
Tail length									
Mean	10.05	10.17			Sex	1	.248	.15	.699
SD	1.37	1.18			Within	70	1.641		
SE	.23	.20							
CV	13.63	11.60							
n	37	35							
Hindfoot length									
Mean	9.03	9.20			Sex	1	.538	1.53	.220
SD	.65	.53			Within	70	.351		
SE	.11	.09							
CV	7.20	5.76							
n	37	35							
Ear length									
Mean	14.60	14.77			Sex	1	.562	.69	.409
SD	.93	.88			Within	70	.816		
SE	.15	.15							
CV	6.37	5.96							
n	37	35							
Tragus length									
Mean	6.00	5.97			Sex	1	.015	.04	.840
SD	.67	.51			Within	70	.357		
SE	.11	.09							
CV	11.17	8.54							
n	37	35							
Forearm length									
Mean	34.65	35.14			Sex	1	4.393	4.35	.041
SD	1.14	.85			Within	70	1.010		
SE	.19	.14							
CV	3.29	2.42							
n	37	35							
Weight									
Mean	8.32	8.87			Sex	1	5.384	8.14	.006
SD	.60	.99			Within	70	.661		
SE	.10	.17							
CV	7.21	11.16							
n	37	35							
Length of digit one									
Mean	7.68	7.54			Sex	1	.317	.97	.327
SD	.58	.56			Within	70	.326		
SE	.10	.10							
CV	7.55	7.43							
n	37	35							

Table 14.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of digit three					
Mean	66.70	67.77			Sex	1	20.54	5.71	.020
SD	2.12	1.63			Within	70	3.60		
SE	.35	.28							
CV	3.18	2.41							
n	37	35							
				Length of digit four					
Mean	49.43	50.23			Sex	1	11.400	6.58	.012
SD	1.24	1.40			Within	70	1.732		
SE	.20	.24							
CV	2.51	2.79							
n	37	35							
				Length of digit five					
Mean	47.27	47.66			Sex	1	2.692	1.30	.259
SD	1.41	1.48			Within	70	2.074		
SE	.23	.25							
CV	2.98	3.11							
n	37	35							
				Tibia length					
Mean	15.08	15.14			Sex	1	.069	.11	.739
SD	.68	.88			Within	70	.615		
SE	.11	.15							
CV	4.51	5.81							
n	37	35							
				Calcar length					
Mean	5.57	5.86			Sex	1	1.508	4.52	.037
SD	.56	.60			Within	70	.334		
SE	.09	.10							
CV	10.05	10.24							
n	37	35							
				Noseleaf length					
Mean	5.05	4.89			Sex	1	.510	1.84	.180
SD	.52	.53			Within	70	.278		
SE	.09	.09							
CV	10.30	10.84							
n	37	35							
				Greatest length of skull					
Mean	22.58	22.59			Sex	1	.001	.00	.944
SD	.43	.37			Within	68	.161		
SE	.07	.07							
CV	1.90	1.64							
n	37	33							
				Condylobasal length					
Mean	21.33	21.36			Sex	1	.012	.08	.784
SD	.46	.33			Within	67	.163		
SE	.08	.06							
CV	2.16	1.54							
n	36	33							

Table 14.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	4.22	4.30			Sex	1	.109	4.12	.046
SD	.13	.19			Within	69	.026		
SE	.02	.03							
CV	3.08	4.42							
n	37	34							
Mastoid breadth									
Mean	9.08	9.01			Sex	1	.068	1.79	.185
SD	.16	.23			Within	67	.038		
SE	.03	.04							
CV	1.76	2.55							
n	36	33							
Breadth of braincase									
Mean	8.39	8.31			Sex	1	.114	3.68	.059
SD	.19	.16			Within	69	.031		
SE	.03	.03							
CV	2.26	1.93							
n	37	34							
Rostral breadth									
Mean	3.62	3.53			Sex	1	.150	6.88	.011
SD	.16	.14			Within	69	.022		
SE	.03	.02							
CV	4.42	3.97							
n	37	34							
Height of braincase									
Mean	8.73	8.75			Sex	1	.002	.03	.871
SD	.26	.24			Within	59	.062		
SE	.05	.05							
CV	2.98	2.74							
n	32	29							
Breadth across the upper molars									
Mean	5.10	5.14			Sex	1	.024	.97	.328
SD	.16	.16			Within	57	.025		
SE	.03	.03							
CV	3.14	3.11							
n	32	27							
Breadth across the upper canines									
Mean	3.71	3.56			Sex	1	.314	14.57	<.001
SD	.15	.15			Within	58	.022		
SE	.03	.03							
CV	4.04	4.21							
n	32	28							
Length of the maxillary toothrow									
Mean	7.75	7.81			Sex	1	.049	1.10	.298
SD	.25	.16			Within	57	.045		
SE	.04	.03							
CV	3.23	2.05							
n	32	27							
Length of the upper molariform toothrow									
Mean	5.82	5.86			Sex	1	.028	1.01	.318
SD	.18	.15			Within	57	.028		
SE	.03	.03							
CV	3.09	2.56							
n	32	27							

Table 14.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Width of the widest molar					
Mean	.92	.96			Sex	1	.022	5.38	.024
SD	.07	.05			Within	58	.004		
SE	.01	.01							
CV	7.61	5.21							
n	32	28							
				Greatest length of the mandible					
Mean	15.71	15.78			Sex	1	.076	.53	.470
SD	.45	.29			Within	69	.145		
SE	.07	.05							
CV	3.86	1.84							
n	37	34							
				Length of the mandibular toothrow					
Mean	8.12	8.07			Sex	1	.033	.66	.419
SD	.20	.25			Within	59	.050		
SE	.04	.05							
CV	2.46	3.10							
n	32	29							
				Length of the coronoid process					
Mean	3.87	3.79			Sex	1	.110	2.38	.128
SD	.21	.22			Within	67	.050		
SE	.03	.04							
CV	5.43	5.80							
n	37	32							

Caatingas where it was usually associated with serrote habitats, but it was locally abundant in open areas of Cerradão or in Cerrado habitats on the Chapada do Araripe. In the Caatingas population, 44% of the 25 captured individuals were males, hence, the sexes occur in equal proportion (Binomial Test, $P > .05$). In contrast, only 21% of the 270 captured specimens in the Cerrado were males; this indicates that males and females occur in significantly different proportions (Binomial Test, $P < .01$) on the Chapada do Araripe.

Morphometric data are reported for Brazilian specimens of *A. g. geoffroyi* by Dobson (1878), Lima (1926), and Cunha Vieira (1942). More recently, Anderson (1957) was unable to detect statistically significant secondary sexual variation in large samples of males and females from Chiapas, Mexico. He did, however, find forearm length and skull length to be significantly different for specimens from South America and Chiapas.

Statistically significant secondary sexual variation in specimens from the Northeast of Brazil is evidenced by three external and five cranial characters; geographic variation between Caatingas and Cerrado habitats is statistically significant for two external and four cranial characters (Table 15).

Subfamily Carolliinae

Carollia perspicillata (Linnaeus, 1758)

This frugivore was abundant and ubiquitous in all habitats of the Caatingas and Cerrado; it was frequently found roosting in man-made structures in association with *Glossophaga soricina.* Of the three subspecies currently recognized, *C. p. perspicillata* is the designation applied to specimens from the Northeast of Brazil (Jones and Carter, 1976). Fruits of *Vismia* composed the major portion of this species' diet on the Chapada do Araripe. Of the 467 captured adult specimens from Cerrado and Cerradão habitats, 42% were males; the proportion of males and females were not statistically equal (Binomial Test, $P < .01$). Although significant, the magnitude of difference between males and females was small; this suggests that factors other than social structure (for example, increased catchability of less maneuverable pregnant females may inflate their

Table 15.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Anoura geoffroyi *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Total length				
Mean	63.73	63.57	65.45	67.85	Area	1	137.287	23.85	<.001
SD	2.57	2.88	2.44	1.84	Sex	1	19.198	3.34	.073
SE	.78	.77	.55	.41	A × S	1	24.901	4.33	.042
CV	4.03	4.53	3.73	2.71	Error	61	5.756		
n	11	14	20	20					
					Hindfoot length				
Mean	10.27	10.79	10.80	10.55	Area	1	.324	.54	.466
SD	.65	.58	1.11	.51	Sex	1	.264	.44	.510
SE	.20	.16	.25	.11	A × S	1	2.219	3.69	.059
CV	6.33	5.38	10.28	4.83	Error	61	.602		
n	11	14	20	20					
					Ear length				
Mean	14.55	14.43	14.35	14.65	Area	1	.003	.00	.949
SD	1.04	1.02	.67	.49	Sex	1	.128	.21	.649
SE	.31	.27	.15	.11	A × S	1	.663	1.08	.302
CV	7.15	7.07	4.67	3.34	Error	61	.611		
n	11	14	20	20					
					Tragus length				
Mean	6.27	5.71	5.90	5.70	Area	1	.571	1.66	.203
SD	.65	.47	.64	.57	Sex	1	2.193	6.36	.014
SE	.20	.13	.14	.13	A × S	1	.490	1.42	.238
CV	10.37	8.23	10.85	10.00	Error	61	.345		
n	11	14	20	20					
					Forearm length				
Mean	42.82	42.14	42.80	43.00	Area	1	2.683	2.46	.122
SD	1.17	.54	1.06	1.21	Sex	1	.861	.79	.378
SE	.35	.14	.24	.27	A × S	1	2.921	2.68	.107
CV	2.73	1.28	2.48	2.81	Error	61	1.091		
n	11	14	20	20					
					Weight				
Mean	15.50	14.36	15.13	15.55	Area	1	2.550	2.07	.155
SD	1.14	1.34	1.00	1.03	Sex	1	1.964	1.60	.211
SE	.34	.36	.22	.23	A × S	1	9.370	7.61	.008
CV	7.35	9.33	6.61	6.62	Error	61	1.231		
n	11	14	20	20					
					Length of digit one				
Mean	8.00	7.93	8.45	8.15	Area	1	1.719	7.27	.009
SD	.45	.48	.51	.49	Sex	1	.526	2.22	.141
SE	.14	.13	.11	.11	A × S	1	.199	.84	.363
CV	5.63	6.05	6.04	6.01	Error	61	.237		
n	11	14	20	20					
					Length of digit three				
Mean	84.91	84.50	85.75	85.50	Area	1	12.918	1.68	.200
SD	4.23	1.99	2.63	2.37	Sex	1	1.656	.22	.644
SE	1.28	.53	.59	.53	A × S	1	.097	.01	.911
CV	4.98	2.36	3.07	2.77	Error	61	7.691		
n	11	14	20	20					

Table 15.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit four									
Mean	62.00	60.36	61.65	61.10	Area	1	.588	.17	.678
SD	1.84	1.74	2.01	1.71	Sex	1	18.330	5.44	.023
SE	.56	.46	.45	.38	A × S	1	4.553	1.35	.250
CV	2.97	2.88	3.26	2.80	Error	61	3.370		
n	11	14	20	20					
Length of digit five									
Mean	54.82	52.71	54.20	53.40	Area	1	.017	.00	.946
SD	1.54	1.94	2.44	1.57	Sex	1	32.144	8.43	.005
SE	.46	.52	.55	.35	A × S	1	6.481	1.70	.197
CV	2.81	3.68	4.50	2.94	Error	61	3.811		
n	11	14	20	20					
Tibia length									
Mean	16.64	16.21	16.55	16.65	Area	1	.465	.88	.353
SD	.67	.43	.89	.75	Sex	1	.395	.74	.392
SE	.20	.11	.20	.17	A × S	1	1.039	1.96	.167
CV	4.03	2.65	5.38	4.50	Error	61	.531		
n	11	14	20	20					
Calcar length									
Mean	3.27	3.21	3.10	2.95	Area	1	.728	2.30	.134
SD	.65	.70	.45	.51	Sex	1	.166	.52	.472
SE	.20	.19	.10	.11	A × S	1	.032	.10	.752
CV	19.88	21.81	14.52	17.29	Error	61	.316		
n	11	14	20	20					
Noseleaf length									
Mean	3.82	3.71	4.10	3.90	Area	1	.833	3.16	.081
SD	.60	.47	.55	.45	Sex	1	.352	1.33	.253
SE	.18	.13	.12	.10	A × S	1	.035	.13	.716
CV	15.71	12.67	13.41	11.54	Error	61	.264		
n	11	14	20	20					
Greatest length of skull									
Mean	24.76	24.34	24.95	24.83	Area	1	1.740	8.04	.006
SD	.43	.34	.62	.38	Sex	1	1.165	5.38	.024
SE	.13	.09	.14	.08	A × S	1	.350	1.62	.209
CV	1.74	1.40	2.48	1.53	Error	61	.217		
n	11	14	20	20					
Condylobasal length									
Mean	24.10	23.67	24.11	24.06	Area	1	.591	2.54	.116
SD	.39	.37	.64	.40	Sex	1	.891	3.84	.055
SE	.12	.10	.14	.09	A × S	1	.532	2.29	.136
CV	1.62	1.53	2.65	1.66	Error	61	.232		
n	11	14	20	20					
Zygomatic breadth									
Mean	10.85	10.83	10.94	10.86	Area	1	.031	.44	.513
SD	.35	.23	.26	.19	Sex	1	.019	.28	.602
SE	.12	.10	.07	.07	A × S	1	.083	.12	.732
CV	3.23	2.12	2.38	1.75	Error	32	.070		
n	8	6	14	8					

Table 15.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Postorbital constriction									
Mean	5.13	5.04	5.19	5.17	Area	1	.130	3.08	.085
SD	.16	.24	.23	.18	Sex	1	.038	.89	.349
SE	.05	.06	.05	.04	A × S	1	.018	.43	.513
CV	3.12	4.76	4.43	3.48	Error	61	.042		
n	11	14	20	20					
Mastoid breadth									
Mean	10.30	10.12	10.36	10.30	Area	1	.217	2.69	.106
SD	.26	.28	.28	.30	Sex	1	.217	2.69	.106
SE	.08	.08	.06	.07	A × S	1	.054	.67	.418
CV	2.52	2.77	2.70	2.91	Error	61	.081		
n	11	14	20	20					
Breadth of braincase									
Mean	9.71	9.61	9.78	9.80	Area	1	.255	5.20	.026
SD	.12	.24	.21	.26	Sex	1	.023	.46	.500
SE	.04	.06	.05	.06	A × S	1	.061	1.25	.268
CV	1.24	2.50	2.15	2.65	Error	61	.049		
n	11	14	20	20					
Rostral breadth									
Mean	4.28	4.14	4.31	4.16	Area	1	.009	.40	.532
SD	.17	.17	.13	.14	Sex	1	.323	14.86	<.001
SE	.05	.05	.03	.03	A × S	1	.000	.00	.988
CV	3.97	4.11	3.02	3.37	Error	61	.022		
n	11	14	20	20					
Height of braincase									
Mean	9.92	9.66	9.89	9.94	Area	1	.214	3.91	.053
SD	.14	.29	.23	.23	Sex	1	.156	2.86	.096
SE	.05	.08	.05	.05	A × S	1	.363	6.64	.013
CV	1.41	3.00	3.33	2.31	Error	61	.055		
n	9	14	20	20					
Breadth across the upper molars									
Mean	6.24	6.15	6.24	6.21	Area	1	.010	.30	.587
SD	.10	.16	.22	.19	Sex	1	.053	1.53	.221
SE	.03	.05	.05	.04	A × S	1	.019	.54	.465
CV	1.60	2.60	3.53	3.06	Error	58	.034		
n	9	13	20	20					
Breadth across the upper canines									
Mean	4.93	4.52	5.02	4.66	Area	1	.166	6.79	.102
SD	.16	.17	.16	.14	Sex	1	2.033	83.24	<.001
SE	.05	.05	.04	.03	A × S	1	.011	.43	.513
CV	3.25	3.76	3.19	3.00	Error	58	.024		
n	9	13	20	20					
Length of the maxillary toothrow									
Mean	9.41	9.19	9.44	9.39	Area	1	.183	2.76	.102
SD	.31	.19	.26	.27	Sex	1	.256	3.88	.054
SE	.11	.05	.06	.06	A × S	1	.114	1.73	.193
CV	3.29	2.07	2.75	2.88	Error	58	.066		
n	9	13	20	20					
Length of the upper molariform toothrow									
Mean	7.87	7.68	7.87	7.87	Area	1	.121	1.95	.168
SD	.27	.25	.24	.25	Sex	1	.125	2.02	.161
SE	.09	.07	.05	.06	A × S	1	.125	2.02	.161
CV	3.43	3.26	3.05	3.18	Error	58	.062		
n	9	13	20	20					

Table 15.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Width of the widest molar					
Mean	1.19	1.17	1.14	1.19	Area	1	.004	1.05	.309
SD	.06	.05	.06	.07	Sex	1	.002	.62	.436
SE	.02	.01	.01	.02	A × S	1	.015	4.01	.050
CV	5.04	4.27	5.26	5.88	Error	58	.004		
n	9	13	20	20					
				Greatest length of the mandible					
Mean	8.08	7.74	8.17	8.20	Area	1	1.113	8.34	.005
SD	.40	.32	.44	.29	Sex	1	.376	2.82	.099
SE	.12	.08	.10	.07	A × S	1	.505	3.78	.056
CV	4.95	4.13	5.39	3.54	Error	61	.134		
n	11	14	20	20					
				Length of the mandibular toothrow					
Mean	9.88	9.62	9.95	9.78	Area	1	.195	3.27	.076
SD	.28	.19	.23	.27	Sex	1	.649	10.90	.002
SE	.09	.05	.05	.06	A × S	1	.030	.50	.483
CV	2.83	1.98	2.31	2.76	Error	58	.060		
n	9	13	20	20					
				Length of the coronoid process					
Mean	4.38	3.92	4.34	4.13	Area	1	.094	1.93	.170
SD	.31	.18	.18	.23	Sex	1	1.713	35.27	<.001
SE	.09	.05	.04	.05	A × S	1	.239	4.92	.030
CV	7.08	4.60	4.15	5.67	Error	61	.049		
n	11	14	20	20					

sample frequency, resulting in unequal sex ratios in large samples) affect the observed proportion of the sexes. In the Caatingas, 47% of the 366 captured adult specimens were males; the sexes occurred in statistically equal frequency (Binomial Test, $P >$ .05).

Although a great deal of information is available on the morphometric characteristics of *C. perspicillata* (see Swanepoel and Genoways, 1979), little has been published on specimens from Brazil. Hahn (1907), Cunha Vieira (1942), Pine (1972), Pirlot (1972), and Taddei (1975*b*) have reported measurements from Brazil, but only Taddei (1975*b*) has performed rigorous statistical analyses. He found that females are larger on the average than males when considering external characters, but statistically different for only four of the 17 characters (head-body length, ear length, forearm length, and length of metacarpal II). Conversely, on the average, males are larger than females when considering a group of 15 cranial characters, but only one character, mastoid breadth, is statistically significantly different. Tamsitt and Valdivieso (1963) state that males and females from Colombia do not differ in size, and that specimens on opposite sides of the Andes do not differ in any character.

Only two external characters (total length and weight) exhibit statistically significant sexual variation in specimens from Northeast Brazil, and no trend is apparent with regard to average size relationships between the sexes. However, when considering cranial characteristics, the sample means of males are generally larger than those of females and for six characters, statistically significant differences are detected (see Table 16). Caatingas specimens have larger sample means than Cerrado specimens for 11 of the 15 analyzed cranial characters; statistically significant differences are indicated for six characters (Table 16). Size trends for external characters are not apparent and only two characters (tragus length and weight) have statistically distinguishable means.

Subfamily Stenodermatinae

Sturnira lilium (E. Geoffroy, 1810)

Of the six tentatively recognized subspecies, *S. l. lilium* is the designation properly applied to specimens from the Northeast of Brazil (Jones and Car-

Table 16.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Carollia perspicillata *males and femlaes from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	72.80	75.65	71.95	73.45	Area	1	46.513	3.49	.066
SD	3.76	4.02	2.80	3.90	Sex	1	94.613	7.09	.009
SE	.84	.90	.63	.87	A × S	1	9.113	.68	.411
CV	5.16	5.31	3.89	5.31	Error	76	13.338		
n	20	20	20	20					
Tail length									
Mean	10.70	11.05	10.75	11.30	Area	1	.450	.15	.700
SD	1.92	1.85	1.68	1.46	Sex	1	4.050	1.34	.250
SE	.43	.41	.38	.33	A × S	1	.200	.07	.797
CV	17.94	16.74	15.63	12.92	Error	76	3.015		
n	20	20	20	20					
Hindfoot length									
Mean	11.85	11.65	11.60	11.75	Area	1	.113	.15	.701
SD	.88	.59	1.05	.91	Sex	1	.013	.02	.898
SE	.20	.13	.23	.20	A × S	1	.613	.81	.372
CV	7.43	5.06	9.05	7.74	Error	76	.759		
n	20	20	20	20					
Ear length									
Mean	19.55	19.30	19.00	19.15	Area	1	2.450	2.46	.121
SD	1.10	1.03	1.03	.81	Sex	1	.050	.05	.823
SE	.25	.23	.23	.18	A × S	1	.800	.80	.373
CV	5.63	5.34	5.42	4.23	Error	76	.996		
n	20	20	20	20					
Tragus length									
Mean	7.70	7.90	8.35	8.30	Area	1	5.513	13.62	<.001
SD	.66	.64	.49	.73	Sex	1	.113	.28	.600
SE	.15	.14	.11	.16	A × S	1	.313	.77	.382
CV	8.57	8.10	5.87	8.80	Error	76	.405		
n	20	20	20	20					
Forearm length									
Mean	42.70	42.95	42.25	42.70	Area	1	2.450	1.11	.295
SD	1.87	1.10	1.37	1.49	Sex	1	2.450	1.11	.295
SE	.42	.25	.31	.33	A × S	1	.200	.09	.764
CV	4.38	2.56	3.24	3.49	Error	76			
n	20	20	20	20					
Weight									
Mean	18.72	20.88	18.50	18.70	Area	1	28.561	6.02	.016
SD	1.35	3.30	1.33	2.11	Sex	1	27.848	5.87	.018
SE	.30	.74	.30	.47	A × S	1	19.208	4.05	.048
CV	7.21	15.80	7.19	11.28	Error	76	4.742		
n	20	20	20	20					
Length of digit one									
Mean	10.85	10.95	11.10	11.30	Area	1	1.800	4.97	.029
SD	.49	.69	.64	.57	Sex	1	.450	1.24	.268
SE	.11	.15	.14	.13	A × S	1	.050	.14	.711
CV	4.52	6.30	5.77	5.04	Error	76	.362		
n	20	20	20	20					

Table 16.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	89.60	90.80	89.65	90.50	Area	1	.313	.03	.860
SD	3.24	2.93	3.63	2.78	Sex	1	21.013	2.10	.151
SE	.72	.66	.81	.62	A × S	1	.613	.06	.805
CV	3.62	3.23	4.05	3.07	Error	76	9.994		
n	20	20	20	20					
Length of digit four									
Mean	65.35	65.50	65.50	65.50	Area	1	.113	.03	.860
SD	1.69	1.85	2.07	1.93	Sex	1	.113	.03	.860
SE	.38	.41	.46	.43	A × S	1	.113	.03	.860
CV	2.59	2.82	3.16	2.95	Error	76	3.573		
n	20	20	20	20					
Length of digit five									
Mean	64.50	64.30	64.00	64.95	Area	1	.113	.03	.871
SD	1.73	2.08	2.56	1.79	Sex	1	2.813	.66	.419
SE	.39	.47	.57	.40	A × S	1	6.613	1.55	.217
CV	2.68	3.23	4.00	2.76	Error	76	4.265		
n	20	20	20	20					
Tibia length									
Mean	19.80	19.60	19.70	19.60	Area	1	.050	.04	.851
SD	.83	.82	1.38	1.54	Sex	1	.450	.32	.574
SE	.19	.19	.31	.34	A × S	1	.050	.04	.851
CV	4.19	4.18	7.01	7.86	Error	76	1.408		
n	20	20	20	20					
Calcar length									
Mean	7.70	7.95	7.50	8.15	Area	1	.000	.000	1.000
SD	.87	1.23	.89	1.04	Sex	1	4.050	3.91	.052
SE	.19	.28	.20	.23	A × S	1	.800	.77	.382
CV	11.30	15.47	11.87	12.76	Error	76	1.036		
n	20	20	20	20					
Noseleaf length									
Mean	6.60	6.65	6.45	6.40	Area	1	.800	1.73	.192
SD	.75	.75	.61	.60	Sex	1	.000	.000	1.000
SE	.17	.17	.14	.13	A × S	1	.050	.11	.743
CV	11.36	11.28	9.46	9.38	Error	76	.462		
n	20	20	20	20					
Greatest length of skull									
Mean	22.26	22.00	22.10	21.77	Area	1	.722	3.99	.049
SD	.43	.28	.45	.52	Sex	1	1.741	9.61	.003
SE	.10	.06	.10	.12	A × S	1	.025	.14	.714
CV	1.93	1.27	2.04	2.39	Error	76	.181		
n	20	20	20	20					
Condylobasal length									
Mean	20.23	20.03	20.05	19.81	Area	1	.780	4.33	.041
SD	.46	.36	.35	.51	Sex	1	.946	5.25	.025
SE	.10	.08	.08	.11	A × S	1	.010	.06	.813
CV	2.27	1.80	1.75	2.57	Error	76	.180		
n	20	20	20	20					
Postorbital constriction									
Mean	5.68	5.55	5.63	5.51	Area	1	.037	.79	.376
SD	.19	.20	.18	.27	Sex	1	.300	6.59	.012
SE	.04	.05	.04	.06	A × S	1	.001	.02	.876
CV	3.35	3.60	3.20	4.90	Error	76	.046		
n	20	20	20	20					

Table 16.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Mastoid breadth					
Mean	10.87	10.86	10.97	10.83	Area	1	.025	.25	.616
SD	.38	.30	.31	.24	Sex	1	.113	1.16	.285
SE	.09	.07	.07	.05	A × S	1	.072	.74	.391
CV	3.50	2.76	2.83	2.22	Error	76	.097		
n	20	20	20	20					
				Breadth of braincase					
Mean	9.75	9.65	9.75	9.73	Area	1	.032	.51	.477
SD	.21	.31	.25	.22	Sex	1	.072	1.15	.287
SE	.05	.07	.06	.05	A × S	1	.032	.51	.477
CV	2.15	3.21	2.56	2.26	Error	76	.063		
n	20	20	20	20					
				Rostral breadth					
Mean	5.19	5.03	5.05	4.94	Area	1	.276	8.21	.005
SD	.17	.21	.19	.16	Sex	1	.351	10.43	.002
SE	.04	.05	.04	.04	A × S	1	.015	.45	.505
CV	3.28	4.17	3.76	3.24	Error	76	.034		
n	20	20	20	20					
				Height of braincase					
Mean	10.87	10.89	10.84	10.85	Area	1	.021	.27	.605
SD	.30	.18	.37	.23	Sex	1	.003	.04	.842
SE	.07	.04	.08	.05	A × S	1	.000	.00	.968
CV	2.76	1.65	3.41	2.12	Error	76	.079		
n	20	20	20	20					
				Breadth across the upper molars					
Mean	3.02	8.07	7.95	7.89	Area	1	.288	5.39	.023
SD	.24	.25	.18	.25	Sex	1	.001	.01	.923
SE	.05	.06	.04	.06	A × S	1	.061	1.13	.291
CV	2.99	3.10	2.26	3.17	Error	76	.053		
n	20	20	20	20					
				Breadth across the upper canines					
Mean	5.30	5.03	5.17	4.98	Area	1	.171	6.44	.013
SD	.18	.13	.16	.17	Sex	1	.035	38.95	<.001
SE	.04	.03	.04	.04	A × S	1	.036	1.36	.247
CV	3.40	2.58	3.09	3.41	Error	76	.027		
n	20	20	20	20					
				Length of the maxillary toothrow					
Mean	7.61	7.54	7.53	7.47	Area	1	.113	2.28	.135
SD	.34	.14	.15	.20	Sex	1	.085	1.71	.194
SE	.08	.03	.03	.05	A × S	1	.000	.000	1.000
CV	4.47	1.86	1.99	2.68	Error	76	.049		
n	20	20	20	20					
				Length of the upper molariform toothrow					
Mean	5.97	5.93	5.79	5.93	Area	1	.162	3.09	.083
SD	.20	.17	.33	.19	Sex	1	.050	.95	.332
SE	.05	.04	.07	.04	A × S	1	.162	3.09	.083
CV	3.35	2.87	5.70	3.20	Error	76	.052		
n	20	20	20	20					
				Width of the widest molar					
Mean	1.61	1.56	1.53	1.54	Area	1	.050	5.47	.022
SD	.11	.09	.07	.10	Sex	1	.013	1.37	.246
SE	.02	.02	.02	.02	A × S	1	.018	1.97	.165
CV	6.83	5.77	4.58	6.49	Error	76	.009		
n	20	20	20	20					

Table 16.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Greatest length of the mandible					
Mean	14.78	14.71	14.73	14.53	Area	1	.253	1.73	.193
SD	.46	.33	.34	.39	Sex	1	.378	2.58	.112
SE	.10	.08	.08	.09	A × S	1	.091	.62	.433
CV	3.11	2.24	2.31	2.68	Error	76	.146		
n	20	20	20	20					
				Length of the mandibular toothrow					
Mean	8.21	8.13	8.13	8.01	Area	1	.181	3.17	.079
SD	.23	.23	.25	.25	Sex	1	.200	3.51	.065
SE	.05	.05	.06	.06	A × S	1	.008	.14	.709
CV	2.80	2.83	3.08	3.12	Error	76	.057		
n	20	20	20	20					
				Length of the coronoid process					
Mean	5.33	5.18	5.25	5.14	Area	1	.072	1.29	.261
SD	.24	.18	.19	.32	Sex	1	.338	6.03	.016
SE	.05	.04	.04	.07	A × S	1	.013	.22	.638
CV	4.50	3.47	3.62	5.23	Error	76	.056		
n	20	20	20	20					

ter, 1976). This frugivore was uncommon in the Caatingas where it was primarily restricted to Caatinga Alta habitats. *S. l. lilium* was also uncommon in both Cerrado and Cerradão habitats of the Chapada do Araripe. Less than 14% of the 22 specimens captured on the Chapada were males; the sex ratio was clearly unequal (Binomial Test, $P < .01$). The small sample from the Caatingas precludes analysis concerning sex ratios. *Vismia* is an important component of this bat's diet on the Chapada do Araripe; no other species of fruit was found in its digestive tract.

An extensive list of authors who have reported morphometric data on *S. lilium* is cited by Swanepoel and Genoways (1979). However, only three authors, Lima (1926), Cunha Vieira (1942), and Taddei (1975*b*), include Brazilian specimens in their work and only Taddei (1975*b*) performs rigorous statistical analyses of individual and secondary sexual variation. He found that *S. lilium* males have larger sample means than females, but that statistically significant variation could not be detected for a suite of 17 external mensural characters. On the other hand, statistically significant secondary sexual variation is apparent for all but two of the 17 cranial characters analyzed, and in all cases, male sample means are larger than female sample means.

The results of a statistical analysis of a sample of *S. lilium* from the Northeast of Brazil yields similar results (see Table 17). Only a single external character (total length) exhibits statistically significant secondary sexual variation and no pattern could be detected when comparing male and female sample means. Males have consistently larger sample means than females for all 16 cranial characters and half of them exhibit statistically significant variation. At least in terms of skull morphology, *S. lilium* is clearly dimorphic with males being larger than females.

Uroderma magnirostrum Davis, 1968

This frugivore is a monotypic species (Jones and Carter, 1976) which was very rare in the Caatingas and on the Chapada do Araripe. The specimens listed by Mares et al. (1981) as *U. bilobatum* from the Northeast of Brazil were in fact *U. magnirostrum*. Other than the original work of Davis (1968), only a few isolated measurements have been reported by Jones et al. (1971) for *U. magnirostrum* from Nicaragua. Selected measurements (after Swanepoel and Genoways, 1979) are reported here for an adult male and female from the Chapada do Araripe and two adult females from the Caatingas (total length: 61, 60, 60, 60; tail length: —, —, —, —; hindfoot length: 11, 11, 10, 11; ear length: 16, 16, 16, 17; greatest length of skull: 23.8, 22.6, 23.0, 23.3; condylobasal length: 22.1, 20.7, 21.2, 21.4; zygomatic breadth: 12.5, 12.4, 12.8, 13.0; postorbital construction: 6.1, 5.9, 5.9, 5.7; breadth of braincase: 9.7, 9.5, 9.4, 9.7; length of the maxillary toothrow: 8.4, 7.8, 8.0, 8.0; and breadth across the

Table 17.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Sturnira lilium *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each external character; the existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050. Due to small sample sizes for the cranial characters, data from both biomes were combined to determine the existence of significant (*P < *.050) secondary sexual variation via a one-way analysis of variance with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Totallength					
Mean	64.33	59.00	60.67	59.95	Area	1	7.629	2.26	.145
SD	1.16	2.00	2.31	1.81	Sex	1	37.795	11.21	.003
SE	.67	1.00	1.33	.42	A × S	1	21.964	6.52	.017
CV	1.80	3.39	3.81	3.02	Error	25	3.371		
n	3	4	3	19					
				Hindfoot length					
Mean	12.00	11.50	11.67	11.74	Area	1	.010	.03	.858
SD	0	.58	.58	.56	Sex	1	.191	.65	.428
SE	0	.29	.33	.13	A × S	1	.335	1.14	.296
CV	0	5.04	4.97	4.77	Error	25	.294		
n	3	4	3	19					
				Ear length					
Mean	15.67	15.75	16.00	15.79	Area	1	.143	.15	.706
SD	1.16	.50	1.00	1.03	Sex	1	.017	.02	.897
SE	.67	.25	.58	.24	A × S	1	.089	.09	.766
CV	7.40	3.17	6.25	6.52	Error	25	.983		
n	3	4	3	19					
				Tragus length					
Mean	6.67	6.75	6.67	6.42	Area	1	.112	.32	.577
SD	.58	.96	.58	.51	Sex	1	.027	.08	.782
SE	.33	.48	.33	.12	A × S	1	.112	.32	.577
CV	8.70	14.22	8.70	7.94	Error	25	.349		
n	3	4	3	19					
				Forearm length					
Mean	43.00	42.00	41.33	42.26	Area	1	2.032	1.05	.315
SD	1.73	1.16	1.16	1.41	Sex	1	.005	.000	.960
SE	1.00	.58	.67	.32	A × S	1	3.842	1.99	.171
CV	4.02	2.76	2.81	3.34	Error	25	1.934		
n	3	4	3	19					
				Weight					
Mean	22.33	21.00	20.33	20.66	Area	1	5.659	1.25	.274
SD	.29	1.23	1.26	2.42	Sex	1	1.050	.23	.634
SE	.17	.61	.73	.55	A × S	1	2.836	.63	.436
CV	1.30	5.86	6.20	11.71	Error	25	4.514		
n	3	4	3	19					
				Length of digit one					
Mean	10.00	10.00	11.00	10.74	Area	1	3.112	4.40	.046
SD	0	1.16	1.00	.81	Sex	1	.071	.10	.753
SE	0	.58	.58	.19	A × S	1	.071	.10	.753
CV	0	11.60	9.09	7.54	Error	25	.707		
n	3	4	3	19					
				Length of digit three					
Mean	88.33	86.75	86.33	88.79	Area	1	.002	.00	.987
SD	1.53	2.75	1.53	2.51	Sex	1	.786	.14	.716
SE	.88	1.38	.88	.58	A × S	1	16.834	2.90	.101
CV	1.73	3.17	1.77	2.83	Error	25	5.810		
n	3	4	3	19					

Table 17.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit four									
Mean	65.33	65.25	65.33	66.16	Area	1	.850	.22	.640
SD	1.53	3.10	1.53	1.77	Sex	1	.567	.15	.702
SE	.88	1.55	.88	.41	A × S	1	.850	.22	.640
CV	2.34	4.75	2.34	2.68	Error	25	3.784		
n	3	4	3	19					
Length of digit five									
Mean	61.33	59.75	60.00	61.58	Area	1	.253	.06	.816
SD	1.53	1.26	1.00	2.39	Sex	1	.000	.00	.998
SE	.88	.63	.58	.54	A × S	1	10.317	2.26	.145
CV	2.49	2.11	1.67	3.88	Error	25	4.562		
n	3	4	3	19					
Tibia length									
Mean	16.67	17.75	17.33	17.68	Area	1	.373	.27	.606
SD	3.22	.96	.58	.75	Sex	1	2.122	1.55	.224
SE	1.86	.48	.33	.17	A × S	1	.554	.40	.530
CV	19.32	5.41	3.35	4.24	Error	25	1.368		
n	3	4	3	19					
Noseleaf length									
Mean	5.33	5.50	5.67	5.05	Area	1	.013	.05	.832
SD	.58	.58	.58	.52	Sex	1	.207	.71	.408
SE	.33	.29	.33	.12	A × S	1	.629	2.16	.154
CV	10.88	10.55	10.23	10.30	Error	25	.291		
n	3	4	3	19					
Greatest length of skull									
Mean	22.20	21.43	21.70	21.74	Sex	1	.194	.97	.335
SD	.42	.29	.10	.48	Within	25	.201		
SE	.30	.14	.06	.11					
CV	1.89	1.35	.46	2.21					
n	2	4	3	18					
Condylobasal length									
Mean	20.35	19.63	19.83	19.59	Sex	1	.804	4.86	.037
SD	.35	.46	.15	.42	Within	25	.166		
SE	.25	.23	.09	.10					
CV	1.72	2.34	.76	2.14					
n	2	4	3	18					
Zygomatic breadth									
Mean	13.65	13.38	13.70	13.45	Sex	1	.242	1.93	.177
SD	.64	.22	.30	.38	Within	25	.126		
SE	.45	.11	.17	.09					
CV	4.69	1.64	2.19	2.83					
n	2	4	3	18					
Postorbital constriction									
Mean	6.20	5.93	6.17	5.88	Sex	1	.341	12.41	.002
SD	.14	.26	.12	.16	Within	25	.027		
SE	.10	.13	.07	.04					
CV	2.26	4.38	1.94	2.72					
n	2	4	3	18					
Mastoid breadth									
Mean	12.40	11.90	12.23	11.91	Sex	1	.637	5.88	.023
SD	.57	.29	.35	.33	Within	25	.108		
SE	.40	.15	.20	.08					
CV	4.60	2.44	2.86	2.77					
n	2	4	3	18					

Table 17.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Breadth of braincase									
Mean	10.41	10.00	10.37	10.20	Sex	1	.191	4.11	.053
SD	.14	.14	.40	.19	Within	25	.046		
SE	.10	.07	.23	.05					
CV	1.34	1.40	3.86	1.86					
n	2	4	3	18					
Rostral breadth									
Mean	7.15	6.75	6.93	6.67	Sex	1	.454	13.60	.001
SD	.07	.17	.25	.18	Within	25	.033		
SE	.05	.09	.15	.04					
CV	.98	2.52	.04	.03					
n	2	4	3	18					
Height of braincase									
Mean	12.00	11.75	12.40	11.83	Sex	1	.741	11.17	.003
SD	.28	.13	.10	.28	Within	25	.066		
SE	.20	.07	.06	.07					
CV	2.33	1.11	.81	2.37					
n	2	4	3	18					
Breadth across the upper molars									
Mean	8.35	8.05	8.27	8.10	Sex	1	.178	3.60	.070
SD	.35	.06	.42	.21	Within	25	.050		
SE	.25	.03	.24	.05					
CV	4.19	.75	5.08	2.59					
n	2	4	3	18					
Breadth across the upper canines									
Mean	6.50	5.95	6.27	5.97	Sex	1	.626	34.01	<.001
SD	0	.10	.15	.14	Within	25	.018		
SE	0	.05	.09	.03					
CV	0	1.68	2.39	2.35					
n	2	4	3	18					
Length of the maxillary toothrow									
Mean	6.90	6.53	6.57	6.59	Sex	1	.061	1.32	.261
SD	.14	.17	.12	.23	Within	25	.043		
SE	.10	.09	.07	.05					
CV	2.03	2.60	1.83	3.49					
n	2	4	3	18					
Length of the upper molariform toothrow									
Mean	5.35	5.15	5.27	5.07	Sex	1	.186	6.40	.018
SD	.07	.19	.15	.18	Within	25	.029		
SE	.05	.10	.09	.04					
CV	1.31	3.69	2.85	3.55					
n	2	4	3	18					
Width of the widest molar									
Mean	1.80	1.70	1.83	1.81	Sex	1	.003	.38	.543
SD	0	.08	.06	.10	Within	25	.009		
SE	0	.04	.03	.02					
CV	0	4.71	3.28	5.52					
n	2	4	3	18					
Greatest length of the mandible									
Mean	14.55	14.00	14.40	14.30	Sex	1	.188	1.03	.320
SD	.35	.41	.10	.46	Within	25	.182		
SE	.25	.20	.06	.10					
CV	2.40	2.93	.69	3.22					
n	2	4	3	18					

Table 17.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of the mandibular toothrow					
Mean	7.90	7.35	7.53	7.35	Sex	1	.444	9.88	.004
SD	.28	.17	.06	.22	Within	25			
SE	.20	.09	.03	.05					
CV	3.54	2.31	.80	2.99					
n	2	4	3	18					
				Length of the coronoid process					
Mean	5.60	5.35	5.53	5.42	Sex	1	.093	2.44	.131
SD	0	.13	.25	.21	Within	25	.038		
SE	0	.07	.15	.05					
CV	0	2.43	4.52	3.87					
n	2	4	3	18					

upper molars: 9.1, 9.2, 9.5, 9.3). These measurements do not differ from the data reported by Swanepoel and Genoways (1979) for *U. magnirostrum.*

Vampyrops lineatus (E. Geoffroy, 1810)

This frugivore was very abundant and ubiquitous in both Caatingas and Cerrado habitats. *Vismia* was a very important component in its diet on the Chapada do Araripe. In the Caatingas, 39% of the 217 captured adult specimens were males; 17% of the 229 captured adult specimens from the Cerrado were males. Both populations exhibited unequal sex ratios (Binomial Test, $P < .01$). Observations at a number of roosting sites in the Caatingas suggested that males often maintain small harems of 7 to 15 females. Single harems occupied each roosting site and individuals within the harem maintained body contact throughout the day. Daily netting records further suggested the existence of male foraging groups. Roosting sites that exclusively contained males were never discovered, perhaps these bachelor males roosted individually and foraged only as a group.

Little has been published on intraspecific variation in *V. lineatus* (Swanepoel and Genoways, 1979) and, although frequently considered a monotypic species (see Koopman, 1979, for an alternate view), some confusion exists concerning its systematic relationship with *V. recifinus.* Lima (1926), Cunha Vieira (1942), and Sanborn (1955) reported some cranial measurements on extremely small samples of *V. lineatus* from Brazil, but no quantitative systematic comparisons were attempted. Taddei (1979) found statistically significant secondary sexual variation in only two of 18 cranial measurements (palate width and basal length) and in five of 18 external characters (forearm, metacarpal of digit III, first phalanx of digit III, third phalanx of digit III and the metacarpal of digit IV) for specimens from northwestern São Paulo, Brazil.

I was able to detect significant secondary sexual variation in nine of 14 external characters but was unable to detect differences in any of the analyzed cranial characters; statistically significant differences between Caatingas and Cerrado biomes exist in four cranial and four external characters (Table 18).

Artibeus concolor Peters, 1865

This frugivore is a monotypic species which was apparently absent from the Caatingas and rare on the Chapada do Araripe. Little has been reported on the morphometric characteristics of *A. concolor* (see Swanepoel and Genoways, 1979) and Cabrera (1917) is the only author who has included a specimen of likely Brazilian origin in his work.

Although samples of *A. concolor* from the Chapada do Araripe are small, they are of sufficient size to allow a statistical analysis of individual and secondary sexual variation in this species (Table 19). There is a clear trend in both external and cranial characters for females to have larger sample means than males; statistically significant secondary sexual variation is exhibited by five external and three cranial characters. In all cases of statistical significance, the female mean value is larger than the male mean value which also suggests sex-related size dimorphism in the population.

Artibeus jamaicensis Leach, 1821

Infraspecific variation in this frugivore is poorly understood for Central and South American populations (see Koopman, 1978, for a discussion of

Table 18.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Vampyrops lineatus *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model 1) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Total length				
Mean	64.40	67.85	63.55	66.70	Area	1	20.000	2.63	.109
SD	2.98	2.60	2.78	2.66	Sex	1	217.800	28.61	<.001
SE	.67	.58	.62	.59	A × S	1	.450	.06	.809
CV	4.63	3.83	4.37	3.99	Error	76	7.612		
n	20	20	20	20					
					Hindfoot length				
Mean	11.20	11.60	11.55	11.90	Area	1	2.113	7.06	.010
SD	.62	.60	.51	.45	Sex	1	2.813	9.40	.003
SE	.14	.13	.11	.10	A × S	1	.013	.04	.839
CV	5.54	5.17	4.42	3.87	Error	76	.299		
n	20	20	20	20					
					Ear length				
Mean	18.05	18.15	17.80	18.15	Area	1	.313	.45	.506
SD	1.05	.67	.89	.67	Sex	1	1.013	1.45	.233
SE	.24	.15	.20	.15	A × S	1	.313	.45	.506
CV	5.82	3.69	5.00	3.69	Error	76	.701		
n	20	20	20	20					
					Tragus length				
Mean	7.15	7.35	7.30	7.10	Area	1	.050	.11	.736
SD	.75	.59	.57	.72	Sex	1	.000	.00	1.000
SE	.17	.13	.13	.16	A × S	1	.800	1.84	.179
CV	10.49	8.03	7.81	10.14	Error	76	.436		
n	20	20	20	20					
					Forearm length				
Mean	47.20	47.45	46.00	47.20	Area	1	10.513	4.09	.047
SD	1.94	2.04	1.12	1.06	Sex	1	10.513	4.09	.047
SE	.43	.46	.25	.24	A × S	1	4.513	1.76	.189
CV	4.11	4.30	2.43	2.25	Error	76	2.570		
n	20	20	20	20					
					Weight				
Mean	23.93	26.44	23.10	26.48	Area	1	3.121	.46	.501
SD	1.32	3.73	1.78	2.90	Sex	1	173.461	25.45	<.001
SE	.30	.84	.40	.65	A × S	1	3.698	.54	.464
CV	5.52	14.11	7.71	10.95	Error	76	6.815		
n	20	20	20	20					
					Length of digit one				
Mean	10.65	10.95	10.60	11.10	Area	1	.050	.09	.759
SD	.75	.76	.75	.64	Sex	1	3.200	6.06	.016
SE	.17	.17	.17	.14	A × S	1	.200	.38	.540
CV	7.04	6.94	7.08	5.77	Error	76	.528		
n	20	20	20	20					
					Length of digit three				
Mean	96.80	97.10	94.00	97.35	Area	1	32.513	3.37	.070
SD	3.49	3.70	2.64	2.41	Sex	1	66.613	6.90	.010
SE	.78	.83	.59	.54	A × S	1	46.513	4.82	.031
CV	3.61	3.81	2.81	2.48	Error	76	9.652		
n	20	20	20	20					

Table 18.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Length of digit four				
Mean	70.95	71.90	69.35	71.05	Area	1	30.013	6.48	.013
SD	2.04	2.55	2.03	1.93	Sex	1	35.113	7.58	.007
SE	.46	.57	.46	.43	A × S	1	2.813	.61	.438
CV	2.88	3.55	2.93	2.72	Error	76	4.635		
n	20	20	20	20					
					Length of digit five				
Mean	65.75	67.25	64.35	66.10	Area	1	32.513	7.10	.009
SD	1.94	2.86	1.90	1.65	Sex	1	52.813	11.54	.001
SE	.44	.64	.43	.37	A × S	1	.313	.07	.795
CV	2.95	4.25	2.95	2.50	Error	76	4.577		
n	20	20	20	20					
					Tibia length				
Mean	18.00	18.35	17.95	18.50	Area	1	.050	.09	.766
SD	.46	.88	.76	.83	Sex	1	4.050	7.24	.009
SE	.10	.20	.17	.19	A × S	1	.200	.36	.552
CV	2.56	4.80	4.23	4.49	Error	76	.559		
n	20	20	20	20					
					Calcar length				
Mean	4.75	4.30	4.25	4.30	Area	1	1.250	3.41	.069
SD	.85	.57	.44	.47	Sex	1	.800	2.18	.144
SE	.19	.13	.10	.10	A × S	1	1.250	3.41	.069
CV	17.89	13.26	10.35	10.93	Error	76	.367		
n	20	20	20	20					
					Noseleaf length				
Mean	6.95	7.00	6.85	7.25	Area	1	.113	.18	.672
SD	.76	.86	.88	.64	Sex	1	1.013	1.63	.206
SE	.17	.19	.20	.14	A × S	1	.613	.99	.324
CV	10.94	12.29	12.85	8.83	Error	76	.623		
n	20	20	20	20					
					Greatest length of skull				
Mean	24.32	24.40	24.38	24.41	Area	1	.018	.09	.762
SD	.46	.37	.56	.35	Sex	1	.061	.31	.579
SE	.10	.08	.13	.08	A × S	1	.013	.06	.801
CV	1.89	1.52	2.30	1.43	Error	76	.195		
n	20	20	20	20					
					Condylobasal length				
Mean	21.90	22.00	21.83	21.89	Area	1	.181	.78	.379
SD	.44	.46	.61	.38	Sex	1	.128	.56	.459
SE	.10	.10	.14	.09	A × S	1	.005	.02	.889
CV	2.01	2.09	2.79	1.74	Error	76	.231		
n	20	20	20	20					
					Zygomatic breadth				
Mean	14.32	14.37	14.25	14.17	Area	1	.365	2.61	.111
SD	.34	.40	.37	.39	Sex	1	.005	.03	.858
SE	.08	.09	.08	.09	A × S	1	.098	.70	.405
CV	2.37	2.78	2.60	2.75	Error	76	.140		
n	20	20	20	20					
					Postorbital constriction				
Mean	6.26	6.29	6.23	6.22	Area	1	.045	1.07	.304
SD	.19	.20	.18	.25	Sex	1	.001	.03	.871
SE	.04	.04	.04	.06	A × S	1	.010	.24	.626
CV	3.04	3.18	2.89	4.02	Error	76	.042		
n	20	20	20	20					

Table 18.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Mastoid breadth				
Mean	12.12	12.22	12.21	12.16	Area	1	.005	.05	.822
SD	.26	.31	.24	.32	Sex	1	.013	.14	.707
SE	.06	.07	.07	.07	A × S	1	.113	1.28	.262
CV	2.15	2.54	1.97	2.63	Error	76	.088		
n	20	20	20	20					
					Breadth of braincase				
Mean	10.51	10.56	10.56	10.58	Area	1	.021	.37	.544
SD	.29	.26	.23	.16	Sex	1	.021	.37	.544
SE	.06	.06	.05	.04	A × S	1	.003	.06	.815
CV	2.76	2.46	2.18	1.51	Error	76	.057		
n	20	20	20	20					
					Rostral breadth				
Mean	7.46	7.42	7.03	6.86	Area	1	4.950	57.83	<.001
SD	.26	.31	.36	.21	Sex	1	.210	2.45	.121
SE	.06	.07	.08	.05	A × S	1	.078	.91	.342
CV	3.49	4.18	5.12	3.06	Error	76	.086		
n	20	20	20	20					
					Height of braincase				
Mean	12.48	12.42	12.44	12.36	Area	1	.045	.63	.429
SD	.23	.31	.29	.24	Sex	1	.105	1.48	.228
SE	.05	.07	.07	.05	A ×S	1	.001	.02	.900
CV	1.84	2.50	2.33	1.94	Error	76	.071		
n	20	20	20	20					
					Breadth across the upper molars				
Mean	10.19	10.40	10.17	10.13	Area	1	.406	5.92	.017
SD	.23	.31	.25	.25	Sex	1	.153	2.23	.139
SE	.05	.07	.06	.06	A × S	1	.325	4.74	.033
CV	2.26	2.98	2.46	2.47	Error	76	.069		
n	20	20	20	20					
					Breadth across the upper canines				
Mean	6.05	6.15	6.09	6.02	Area	1	.045	1.08	.302
SD	.22	.23	.15	.21	Sex	1	.006	.15	.703
SE	.05	.05	.03	.05	A × S	1	.153	3.67	.059
CV	3.64	3.74	2.46	3.49	Error	76	.042		
n	20	20	20	20					
					Length of the maxillary toothrow				
Mean	8.59	8.75	8.76	8.62	Area	1	.010	.11	.738
SD	.33	.32	.28	.27	Sex	1	.001	.01	.911
SE	.07	.07	.06	.06	A × S	1	.435	4.83	.031
CV	3.84	3.66	3.20	3.13	Error	76	.090		
n	20	20	20	20					
					Length of the upper molariform toothrow				
Mean	7.09	7.16	7.05	7.98	Area	1	.231	3.95	.050
SD	.26	.28	.21	.20	Sex	1	.000	.00	.963
SE	.06	.06	.05	.05	A × S	1	.105	1.80	.184
CV	3.67	3.91	2.98	2.51	Error	76	.059		
n	20	20	20	20					
					Width of the widest molar				
Mean	2.51	2.53	2.42	2.45	Area	1	.145	8.03	.006
SD	.11	.13	.14	.16	Sex	1	.018	1.00	.320
SE	.02	.03	.03	.04	A × S	1	.001	.03	.868
CV	4.38	5.14	5.79	6.53	Error	76	.018		
n	20	20	20	20					

Table 18.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Greatest length of the mandible				
Mean	16.62	16.74	16.49	16.49	Area	1	.722	4.73	.033
SD	.48	.28	.45	.32	Sex	1	.072	.47	.494
SE	.11	.06	.10	.07	A × S	1	.085	.55	.459
CV	2.89	1.67	2.73	1.94	Error	76	.153		
n	20	20	20	20					
					Length of the mandibular toothrow				
Mean	9.53	9.60	9.54	9.46	Area	1	.098	1.25	.267
SD	.26	.33	.25	.26	Sex	1	.001	.01	.937
SE	.06	.08	.06	.06	A × S	1	.113	1.44	.235
CV	2.73	3.44	2.62	2.75	Error	76	.078		
n	20	20	20	20					
					Length of the coronoid process				
Mean	5.69	5.87	5.76	5.74	Area	1	.018	.28	.595
SD	.25	.25	.29	.21	Sex	1	.128	2.03	.159
SE	.06	.06	.07	.05	A × S	1	.181	2.86	.095
CV	4.39	4.26	5.03	3.66	Error	76	.063		
n	20	20	20	20					

Table 19.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Artibeus concolor *males and females from the Cerrado biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Total length				
Mean			58.33	61.50	Sex	1	30.083	7.02	.024
SD			2.07	2.07	Within	10	4.283		
SE			.84	.85					
CV			3.55	3.37					
n			6	6					
					Hindfoot length				
Mean			10.33	10.33	Sex	1	.000	.000	1.000
SD			.52	.52	Within	10	.267		
SE			.21	.21					
CV			5.03	5.03					
n			6	6					
					Ear length				
Mean			17.00	17.00	Sex	1	.000	.000	1.000
SD			.63	.63	Within	10	.400		
SE			.26	.26					
CV			3.71	3.71					
n			6	6					
					Tragus length				
Mean			6.50	7.50	Sex	1	3.000	6.00	.034
SD			.84	.55	Within	10	.500		
SE			.34	.22					
CV			12.92	7.33					
n			6	6					

Table 19.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Forearm length					
Mean			47.00	47.33	Sex	1	.333	.09	.771
SD			2.19	1.63	Within	10	3.733		
SE			.89	.67					
CV			4.66	3.44					
n			6	6					
				Weight					
Mean			18.42	21.42	Sex	1	27.000	16.45	.002
SD			.86	1.59	Within	10	1.642		
SE			.35	.65					
CV			4.67	7.42					
n			6	6					
				Length of digit one					
Mean			10.67	10.17	Sex	1	.750	1.22	.296
SD			.52	.98	Within	10	.617		
SE			.21	.41					
CV			4.87	9.64					
n			6	6					
				Length of digit three					
Mean			96.33	99.50	Sex	1	30.083	2.02	.186
SD			4.68	2.81	Within	10	14.883		
SE			1.91	1.15					
CV			4.86	2.82					
n			6	6					
				Length of digit four					
Mean			73.17	73.50	Sex	1	.333	.04	.850
SD			3.49	2.35	Within	10	8.833		
SE			1.42	.96					
CV			4.77	3.20					
n			6	6					
				Length of digit five					
Mean			69.17	68.67	Sex	1	.750	.07	.794
SD			4.12	1.97	Within	10	10.417		
SE			1.68	.80					
CV			5.96	2.87					
n			6	6					
				Tibia length					
Mean			18.50	18.33	Sex	1	.083	.08	.787
SD			1.05	1.03	Within	10	1.083		
SE			.43	.42					
CV			5.68	5.62					
n			6	6					
				Calcar length					
Mean			5.67	6.67	Sex	1	3.000	6.43	.030
SD			.82	.52	Within	10	.467		
SE			.33	.21					
CV			14.46	7.80					
n			6	6					
				Noseleaf length					
Mean			6.67	7.33	Sex	1	1.333	5.00	.049
SD			.52	.52	Within	10	.267		
SE			.21	.21					
CV			7.80	7.09					
n			6	6					

Table 19.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Greatest length of skull									
Mean			21.22	21.23	Sex	1	.001	.00	.957
SD			.40	.40	Within	9	.160		
SE			.18	.17					
CV			1.89	1.88					
n			5	6					
Condylobasal length									
Mean			18.84	19.18	Sex	1	.322	3.21	.107
SD			.35	.29	Within	9	.100		
SE			.16	.12					
CV			1.86	1.51					
n			5	6					
Zygomatic breadth									
Mean			13.00	13.17	Sex	1	.076	1.19	.304
SD			.19	.29	Within	9	.064		
SE			.08	.12					
CV			1.46	2.20					
n			5	6					
Postorbital constriction									
Mean			5.44	5.47	Sex	1	.002	.20	.662
SD			.09	.10	Within	9	.010		
SE			.04	.04					
CV			1.65	1.83					
n			5	6					
Mastoid breadth									
Mean			11.12	11.53	Sex	1	.466	11.00	.009
SD			.13	.25	Within	9	.042		
SE			.06	.10					
CV			1.17	2.17					
n			5	6					
Breadth of braincase									
Mean			9.90	9.80	Sex	1	.027	.35	.568
SD			.31	.25	Within	9	.078		
SE			.14	.10					
CV			3.13	2.55					
n			5	6					
Rostral breadth									
Mean			6.96	7.43	Sex	1	.611	14.27	.004
SD			.20	.22	Within	9	.043		
SE			.09	.09					
CV			2.87	2.96					
n			5	6					
Height of braincase									
Mean			11.60	11.42	Sex	1	.092	1.02	.339
SD			.27	.32	Within	9	.090		
SE			.12	.13					
CV			2.33	2.80					
n			5	6					
Breadth across the upper molars									
Mean			9.14	9.48	Sex	1	.322	6.29	.034
SD			.20	.25	Within	9	.051		
SE			.09	.10					
CV			2.19	2.64					
n			5	6					

Table 19.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
			Breadth across the upper canines						
Mean			5.78	5.87	Sex	1	.021	.24	.639
SD			.21	.35	Within	9	.087		
SE			.09	.14					
CV			3.63	5.96					
n			5	6					
			Length of the maxillary toothrow						
Mean			6.82	7.02	Sex	1	.106	2.28	.165
SD			.26	.17	Within	9	.046		
SE			.12	.07					
CV			3.81	2.42					
n			5	6					
			Length of the upper molariform toothrow						
Mean			5.68	6.02	Sex	1	.309	5.00	.052
SD			.18	.29	Within	9	.062		
SE			.08	.12					
CV			3.17	4.82					
n			5	6					
			Width of the widest molar						
Mean			2.38	2.45	Sex	1	.013	1.91	.200
SD			.08	.08	Within	9	.007		
SE			.04	.03					
CV			3.36	3.26					
n			5	6					
			Greatest length of the mandible						
Mean			13.84	13.98	Sex	1	.056	.55	.478
SD			.37	.27	Within	9	.102		
SE			.16	.11					
CV			2.67	1.93					
n			5	6					
			Length of the mandibular toothrow						
Mean			7.52	7.63	Sex	1	.035	.45	.519
SD			.37	.18	Within	9	.078		
SE			.17	.07					
CV			4.92	2.36					
n			5	6					
			Length of the coronoid process						
Mean			5.56	5.65	Sex	1	.022	.57	.468
SD			.11	.24	Within	9	.039		
SE			.05	.10					
CV			1.98	4.25					
n			5	6					

probable systematic relations), hence it seems premature to assign a subspecific designation to Northeast Brazilian populations. This species was abundant and ubiquitous in both Cerrado and Cerradão habitats on the Chapada do Araripe; *Vismia* was the predominant fruit in its diet there. It was present in the Caatingas and reached its highest density on or near serrotes. The proportion of males was not equal to the proportion of females within either Caatingas or Cerrado biomes (Binomial Tests, $P < .01$). Twenty-eight percent of the 204 captured adult specimens from the Caatingas were males, whereas 40% of the 270 captured adult specimens from the Cerrado were males.

A plethora of references including morphometric data on *A. jamaicensis* are cited by Swanepoel and Genoways (1979), but only Rehn (1900, 1902), G. M. Allen (1908), Andersen (1908), and Cunha Vieira (1942) report measurements from Brazilian specimens. Davis (1970) examined individual, secondary sexual, and geographic variation in specimens of *A. jamaicensis* from Middle America, but no one has examined variation in a statistically rigorous manner for South American specimens.

Table 20 details the results of statistical analyses of individual, secondary sexual and geographic variation in Brazilian specimens of *A. jamaicensis* from Caatingas and Cerrado biomes. Statistically significant geographic variation was detected for seven external and ten cranial characters; in all of these cases, the sample means for Caatingas specimens are larger than the sample means for Cerrado specimens. These two distinct yet geographically proximate populations are clearly dimorphic. Secondary sexual variation is not apparent for *A. jamaicensis* when considering external morphometric variables (only weight is statistically significant); however, males have larger sample means than females for eleven cranial characters and the variation is statistically significant for five of them. Females, on the other hand, were never larger than males when considering sample means for cranial characters. There is then, appreciable secondary sexual variation exhibited by cranial characters and strong evidence for sexual dimorphism for size with males being larger than females. This is unlike the results obtained by Davis (1970) who found no significant secondary sexual variation in samples from numerous localities in Central America. This failure to detect significant variation was most likely caused by the large quantity of variation attributable to geographic heterogeneity in Davis' samples which was not statistically removed from his analysis of secondary sexual variation.

Artibeus lituratus (Olfers, 1818)

Infraspecific relationships for this species are poorly understood at the present (see for example Koopman, 1976); as such, it is best to avoid using a provisional subspecific appellation for populations from the Brazilian Northeast. This frugivore was widespread and abundant in both Cerrado and Cerradão habitats; *Vismia* was the predominant fruit in its diet on the Chapada do Araripe. It was widespread but uncommon in the Caatingas. Within both Caatingas and Cerrado biomes, the sexes occurred in equal frequency (Binomial Test, $P > .05$). Of the 44 captured adult specimens from the Caatingas, 45% were males. Similarly, 58% of the 366 captured adults from the Cerrado were males.

Morphometric data on *A. lituratus* appears in the literature many times (see Swanepoel and Genoways, 1979), but only G. M. Allen (1908), Andersen (1908), Cunha Vieira (1942), and Pirlot (1972) consider Brazilian specimens. Secondary sexual variation in *A. lituratus* was examined by Anderson (1960) and Tamsitt and Valdivieso (1963), but only the former performed statistical analyses, and there was no significant secondary sexual variation detected in that study. Geographic variation in mensural characters for *A. lituratus* was examined by Dalquest (1950) and Tamsitt and Valdivieso (1963) but no statistical results are reported. Further, individual variation in morphometric characters has not been investigated in this species.

The results of a statistical analysis of individual, secondary sexual, and geographic variation for populations of *A. lituratus* from Cerrado and Caatingas biomes are summarized in Table 21. Four external characters exhibit statistically significant secondary sexual variation, whereas none of the cranial characters exhibit statistical differences between males and females. Obvious trends in mean values for males and females are not observed; trends in mean values for Caatingas and Cerrado populations are also not evident. However, a group of five cranial characters exhibits statistically significant secondary sexual variation in which four male mean values are larger than the comparable female mean values. Only a single external character shows statistically significant sexual variation. Secondary sexual variation occurs in populations of *A. lituratus* but is not extensive.

Subfamily Desmodontinae

Desmodus rotundus (E. Geoffroy, 1810)

Of the two extant subspecies, *D. r. rotundus* is the designation properly applied to Northeast Brazilian populations of this sanguinivore (Jones and Carter, 1976). It was common in the Caatingas where it was locally abundant on serrotes. Of the 365 captured adult specimens from the Caatingas, 45% were males; as such the sexes occurred in statistically indistinguishable proportions (Binomial Test, $P > .05$). It was rare in Cerrado and Cerradão habitats of the Chapada do Araripe, perhaps due to the paucity of livestock and other large wild mammals.

Table 20.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Artibeus jamaicensis *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	74.85	75.85	73.20	73.75	Area	1	70.313	7.36	.008
SD	2.98	3.08	3.12	3.18	Sex	1	12.013	1.26	.266
SE	.67	.69	.70	.71	A × S	1	1.013	.11	.746
CV	3.98	4.06	4.26	4.31	Error	76	9.553		
n	20	20	20	20					
Hindfoot length									
Mean	13.25	13.65	13.30	13.35	Area	1	.313	.43	.513
SD	.79	1.09	.66	.81	Sex	1	1.013	1.40	.241
SE	.18	.24	.15	.18	A × S	1	.613	.85	.361
CV	5.96	7.99	4.96	6.07	Error	76	.724		
n	20	20	20	20					
Ear length									
Mean	20.55	20.55	20.40	20.35	Area	1	.613	.65	.421
SD	.95	.95	.88	1.09	Sex	1	.013	.01	.908
SE	.21	.21	.20	.24	A × S	1	.013	.01	.908
CV	4.62	4.62	4.31	5.36	Error	76	.938		
n	20	20	20	20					
Tragus length									
Mean	8.15	8.20	8.10	8.10	Area	1	.113	.34	.563
SD	.59	.62	.55	.55	Sex	1	.013	.04	.847
SE	.13	.14	.12	.12	A × S	1	.013	.04	.847
CV	7.24	7.56	6.70	6.79	Error	76	.334		
n	20	20	20	20					
Forearm length									
Mean	58.95	59.45	57.40	57.20	Area	1	72.200	16.43	<.001
SD	2.16	1.47	2.14	2.48	Sex	1	.450	.10	.750
SE	.48	.33	.48	.56	A × S	1	2.450	.56	.458
CV	3.66	2.47	3.73	4.34	Error	76	4.393		
n	20	20	20	20					
Weight									
Mean	40.98	46.38	39.40	41.03	Area	1	239.778	14.13	<.001
SD	3.48	5.84	2.08	4.17	Sex	1	246.753	14.54	<.001
SE	.78	1.31	.46	.93	A × S	1	71.253	4.20	.044
CV	8.49	12.59	5.28	10.16	Error	76	16.970		
n	20	20	20	20					
Length of digit one									
Mean	11.65	11.70	11.75	11.45	Area	1	.113	.19	.666
SD	.75	.87	.72	.76	Sex	1	.313	.52	.472
SE	.17	.19	.16	.17	A × S	1	.613	1.02	.315
CV	6.44	7.44	6.13	6.64	Error	76	.598		
n	20	20	20	20					
Length of digit three									
Mean	113.30	114.45	111.65	111.30	Area	1	115.200	5.89	.018
SD	4.23	4.81	3.58	4.94	Sex	1	3.200	.16	.687
SE	.95	1.08	.80	1.11	A × S	1	11.250	.58	.451
CV	3.73	4.20	3.21	4.44	Error	76	19.551		
n	20	20	20	20					

Table 20.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit four									
Mean	86.45	87.85	84.95	85.25	Area	1	18.050	7.81	.007
SD	2.74	3.27	2.52	4.30	Sex	1	14.450	1.34	.250
SE	.61	.73	.56	.96	A × S	1	6.050	.56	.456
CV	3.17	3.72	2.97	5.04	Error	76	10.766		
n	20	20	20	20					
Length of digit five									
Mean	79.80	81.45	77.70	77.65	Area	1	174.050	22.77	<.001
SD	2.44	1.64	2.03	4.22	Sex	1	12.800	1.67	.200
SE	.55	.37	.45	.94	A × S	1	14.450	1.89	.173
CV	3.06	2.01	2.61	5.43	Error	76	7.643		
n	20	20	20	20					
Tibia length									
Mean	23.60	23.40	23.05	22.80	Area	1	6.613	3.93	.051
SD	1.50	.60	1.23	1.61	Sex	1	1.013	.60	.440
SE	.34	.13	.28	.36	A × S	1	.013	.01	.932
CV	6.36	2.56	5.34	7.06	Error	76	1.681		
n	20	20	20	20					
Calcar length									
Mean	6.45	6.50	6.00	6.25	Area	1	2.450	2.92	.091
SD	.83	1.05	.92	.85	Sex	1	.450	.54	.466
SE	.19	.24	.21	.19	A × S	1	.200	.24	.627
CV	12.87	16.15	15.33	13.60	Error	76	.838		
n	20	20	20	20					
Noseleaf length									
Mean	6.80	6.45	6.50	6.45	Area	1	.450	1.22	.273
SD	.62	.51	.51	.76	Sex	1	.800	2.16	.145
SE	.14	.11	.12	.17	A × S	1	.450	1.22	.273
CV	9.12	7.91	7.85	11.78	Error	76	.370		
n	20	20	20	20					
Greatest length of skull									
Mean	27.68	27.61	27.30	26.96	Area	1	5.305	17.47	.001
SD	.53	.43	.51	.70	Sex	1	.841	2.77	.100
SE	.12	.10	.11	.16	A × S	1	.338	1.11	.295
CV	1.91	1.56	1.87	2.60	Error	76	.304		
n	20	20	20	20					
Condylobasal length									
Mean	24.41	24.37	24.17	23.91	Area	1	2.485	9.49	.003
SD	.59	.38	.41	.62	Sex	1	.465	1.78	.187
SE	.13	.08	.09	.14	A × S	1	.253	.97	.329
CV	2.42	1.56	1.70	2.59	Error	76	.262		
n	20	20	20	20					
Zygomatic breadth									
Mean	17.20	17.07	16.87	16.62	Area	1	3.121	17.05	<.001
SD	.38	.30	.42	.58	Sex	1	.761	4.16	.045
SE	.08	.07	.09	.13	A × S	1	.061	.33	.567
CV	2.21	1.76	2.49	3.49	Error	76	.183		
n	20	20	20	20					
Postorbital constriction									
Mean	6.99	6.92	6.99	6.82	Area	1	.050	1.03	.312
SD	.24	.15	.28	.20	Sex	1	.265	5.47	.022
SE	.05	.03	.06	.04	A × S	1	.050	1.03	.312
CV	2.43	2.17	4.01	2.93	Error	76	.048		
n	20	20	20	20					

Table 20.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Mastoid breadth					
Mean	15.08	14.90	14.95	14.60	Area	1	.925	7.15	.009
SD	.31	.34	.40	.38	Sex	1	1.458	11.28	.001
SE	.07	.08	.09	.09	A × S	1	.144	1.12	.294
CV	2.06	2.28	2.68	2.60	Error	76	.129		
n	20	20	20	20					
				Breadth of braincase					
Mean	12.28	12.27	12.26	12.07	Area	1	.253	4.38	.040
SD	.19	.28	.22	.26	Sex	1	.190	3.29	.074
SE	.04	.06	.05	.06	A × S	1	.171	2.96	.089
CV	1.55	2.28	1.79	2.15	Error	76	.058		
n	20	20	20	20					
				Rostral breadth					
Mean	8.88	9.02	8.98	8.76	Area	1	.128	1.54	.218
SD	.35	.18	.25	.34	Sex	1	.032	.39	.537
SE	.08	.04	.06	.08	A × S	1	.648	7.80	.007
CV	3.94	2.00	2.78	3.88	Error	76	.083		
n	20	20	20	20					
				Height of braincase					
Mean	14.21	14.06	13.99	13.86	Area	1	.882	7.04	.010
SD	.29	.22	.37	.49	Sex	1	.392	3.13	.081
SE	.06	.05	.08	.11	A × S	1	.005	.04	.850
CV	2.04	1.56	2.64	3.54	Error	76	.125		
n	20	20	20	20					
				Breadth across the upper molars					
Mean	12.44	12.34	12.38	11.99	Area	1	.841	6.82	.011
SD	.34	.22	.34	.46	Sex	1	1.201	9.74	.003
SE	.08	.05	.08	.10	A × S	1	.421	3.41	.069
CV	2.73	1.78	2.75	3.84	Error	76	.123		
n	20	20	20	20					
				Breadth across the upper canines					
Mean	7.95	7.98	7.94	7.53	Area	1	1.035	14.22	<.001
SD	.28	.22	.28	.30	Sex	1	.741	10.18	.002
SE	.06	.05	.06	.07	A × S	1	.990	13.60	<.001
CV	3.52	2.76	3.53	3.98	Error	76	.073		
n	20	20	20	20					
				Length of the maxillary toothrow					
Mean	9.83	9.78	9.91	9.60	Area	1	.055	.68	.411
SD	.26	.30	.29	.29	Sex	1	.630	7.82	.007
SE	.06	.07	.06	.06	A × S	1	.325	4.04	.408
CV	2.65	3.07	2.93	3.02	Error	76	.081		
n	20	20	20	20					
				Length of the upper molariform toothrow					
Mean	8.09	8.20	8.10	7.83	Area	1	.648	10.12	.002
SD	.22	.25	.30	.24	Sex	1	.145	2.26	.137
SE	.05	.06	.07	.05	A × S	1	.722	11.28	.001
CV	2.72	3.05	3.70	3.07	Error	76	.064		
n	20	20	20	20					
				Width of the widest molar					
Mean	3.64	3.62	3.76	3.60	Area	1	.050	2.06	.156
SD	.11	.16	.18	.17	Sex	1	.145	5.95	.017
SE	.03	.04	.04	.04	A × S	1	.098	4.03	.048
CV	3.02	4.42	4.79	4.72	Error	76	.024		
n	20	20	20	20					

Table 20.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Greatest length of the mandible					
Mean	18.92	18.81	18.75	18.63	Area	1	.595	4.34	.041
SD	.44	.32	.28	.42	Sex	1	.253	1.85	.178
SE	.10	.07	.06	.09	A × S	1	.001	.01	.928
CV	2.33	1.70	1.49	2.25	Error	76	.137		
n	20	20	20	20					
				Length of the mandibular toothrow					
Mean	10.70	10.73	10.60	10.38	Area	1	1.035	13.07	.001
SD	.20	.20	.37	.32	Sex	1	.171	2.16	.146
SE	.05	.04	.08	.07	A × S	1	.325	4.11	.046
CV	1.87	1.86	3.49	3.08	Error	76	.079		
n	20	20	20	20					
				Length of the coronoid process					
Mean	8.14	8.11	8.07	8.09	Area	1	.045	.55	.460
SD	.29	.28	.32	.25	Sex	1	.001	.01	.907
SE	.07	.06	.07	.06	A × S	1	.015	.18	.669
CV	3.56	3.45	3.97	3.09	Error	76	.082		
n	20	20	20	20					

Table 21.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Artibeus lituratus *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean	88.55	90.40	86.65	91.20	Area	1	6.05	.41	.524
SD	3.52	4.33	3.30	4.11	Sex	1	204.80	13.90	<.001
SE	.79	.97	.74	.92	A × S	1	36.45	2.47	.120
CV	3.98	4.79	3.81	4.51	Error	76	14.73		
n	20	20	20	20					
				Hindfoot length					
Mean	16.65	16.25	16.50	16.30	Area	1	.050	.05	.828
SD	1.09	1.02	.95	1.03	Sex	1	1.800	1.72	.194
SE	.24	.23	.21	.23	A × S	1	.200	.19	.663
CV	6.55	6.28	5.76	6.32	Error	76	1.046		
n	20	20	20	20					
				Ear length					
Mean	22.65	22.30	22.10	22.70	Area	1	.113	.06	.800
SD	1.09	1.84	.64	1.42	Sex	1	.313	.18	.674
SE	.24	.41	.14	.32	A × S	1	4.513	2.58	.112
CV	4.81	8.25	2.90	6.26	Error	76	1.748		
n	20	20	20	20					
				Tragus length					
Mean	8.50	8.50	8.55	8.75	Area	1	.450	.93	.337
SD	.61	.61	.89	.64	Sex	1	.200	.41	.522
SE	.14	.14	.20	.14	A × S	1	.200	.41	.522
CV	7.18	7.18	10.41	7.31	Error	76	.483		
n	20	20	20	20					

Table 21.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Forearm length									
Mean	70.60	71.90	69.75	70.95	Area	1	16.200	1.82	.182
SD	2.56	3.87	2.63	2.69	Sex	1	31.250	3.51	.065
SE	.57	.86	.59	.60	A × S	1	.050	.01	.941
CV	3.63	5.38	3.77	3.79	Error	76	8.912		
n	20	20	20	20					
Weight									
Mean	69.35	76.15	66.88	74.13	Area	1	101.250	2.36	.128
SD	4.74	7.95	3.93	8.37	Sex	1	987.013	23.05	<.001
SE	1.06	1.78	.88	1.87	A × S	1	1.013	.02	.878
CV	6.83	10.44	5.88	11.29	Error	76	42.816		
n	20	20	20	20					
Length of digit one									
Mean	14.30	14.25	14.25	14.55	Area	1	.313	.24	.625
SD	1.08	1.07	1.29	1.10	Sex	1	.313	.24	.625
SE	.24	.24	.29	.25	A × S	1	.613	.47	.494
CV	7.55	7.51	9.05	7.56	Error	76	1.298		
n	20	20	20	20					
Length of digit three									
Mean	140.90	142.65	141.20	142.50	Area	1	.113	.00	.952
SD	4.41	6.83	5.35	5.35	Sex	1	46.513	1.51	.223
SE	.99	1.53	1.20	1.20	A × S	1	1.013	.03	.857
CV	3.13	4.79	3.79	3.75	Error	76	30.823		
n	20	20	20	20					
Length of digit four									
Mean	106.30	107.15	105.40	106.50	Area	1	12.013	.56	.455
SD	4.66	5.43	3.58	4.61	Sex	1	19.013	.89	.348
SE	1.04	1.22	.80	1.03	A × S	1	.313	.01	.904
CV	4.38	5.07	3.40	4.39	Error	76	21.297		
n	20	20	20	20					
Length of digit five									
Mean	98.65	100.05	97.95	99.45	Area	1	8.450	.42	.521
SD	3.72	5.95	3.63	4.33	Sex	1	42.050	2.07	.154
SE	.83	1.33	.81	.97	A × S	1	.050	.00	.961
CV	3.77	5.95	3.71	4.35	Error	76	20.308		
n	20	20	20	20					
Tibia length									
Mean	27.15	27.60	26.95	27.75	Area	1	.013	.01	.929
SD	1.76	1.14	1.05	.91	Sex	1	7.813	4.95	.029
SE	.39	.26	.21	.21	A × S	1	.613	.39	.535
CV	5.48	4.13	3.90	3.28	Error	76	1.579		
n	20	20	20	20					
Calcar length									
Mean	8.25	7.90	8.95	8.45	Area	1	7.813	8.80	.004
SD	.97	.91	.95	.95	Sex	1	3.613	4.07	.047
SE	.22	.20	.21	.21	A × S	1	.113	.13	.723
CV	11.76	11.52	10.61	11.24	Error	76	.888		
n	20	20	20	20					
Noseleaf length									
Mean	8.30	8.25	8.20	8.35	Area	1	.000	.00	1.000
SD	.66	1.07	.83	.59	Sex	1	.050	.08	.783
SE	.15	.24	.19	.13	A × S	1	.200	.31	.582
CV	7.95	12.97	10.12	7.07	Error	76	.654		
n	20	20	20	20					

Table 21.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Greatest length of skull					
Mean	31.30	31.33	30.87	31.16	Area	1	1.800	3.18	.079
SD	.62	.82	.79	.76	Sex	1	.512	.90	.345
SE	.14	.18	.18	.17	A × S	1	.338	.60	.442
CV	1.98	2.62	2.56	2.44	Error	76	.566		
n	20	20	20	20					
				Condylobasal length					
Mean	27.87	27.90	27.33	27.68	Area	1	2.926	6.83	.001
SD	.53	.73	.60	.73	Sex	1	.703	1.64	.204
SE	.12	.16	.14	.16	A × S	1	.496	1.16	.285
CV	1.90	2.62	2.20	2.64	Error	76	.428		
n	20	20	20	20					
				Zygomatic breadth					
Mean	19.07	18.87	18.66	18.91	Area	1	.722	2.32	.132
SD	.49	.75	.46	.49	Sex	1	.013	.04	.842
SE	.11	.17	.10	.11	A × S	1	1.013	3.25	.075
CV	2.57	3.97	2.47	2.59	Error	76	.311		
n	20	20	20	20					
				Postorbital constriction					
Mean	6.73	6.71	6.72	6.68	Area	1	.010	.13	.720
SD	.25	.27	.32	.27	Sex	1	.021	.27	.605
SE	.06	.06	.07	.06	A × S	1	.003	.04	.842
CV	3.71	4.02	4.76	4.04	Error	76	.078		
n	20	20	20	20					
				Mastoid breadth					
Mean	16.82	16.64	16.62	16.70	Area	1	.091	.48	.491
SD	.53	.46	.39	.34	Sex	1	.055	.29	.592
SE	.12	.10	.09	.08	A × S	1	.351	1.84	.179
CV	3.15	2.76	2.35	2.04	Error	76	.190		
n	20	20	20	20					
				Breadth of braincase					
Mean	13.36	13.36	13.48	13.41	Area	1	.153	1.13	.290
SD	.27	.36	.45	.37	Sex	1	.028	.21	.650
SE	.06	.08	.10	.08	A × S	1	.021	.16	.694
CV	2.02	2.69	3.34	2.76	Error	76	.135		
n	20	20	20	20					
				Rostral breadth					
Mean	10.17	10.02	9.82	10.02	Area	1	.780	5.12	.027
SD	.47	.42	.39	.26	Sex	1	.210	1.38	.244
SE	.10	.09	.09	.06	A × S	1	.210	1.38	.244
CV	4.64	4.15	3.97	2.59	Error	76	.153		
n	20	20	20	20					
				Height of braincase					
Mean	15.77	15.52	15.64	15.56	Area	1	.046	.19	.661
SD	.48	.48	.56	.42	Sex	1	.553	2.33	.131
SE	.11	.11	.13	.09	A × S	1	.153	.64	.425
CV	3.04	3.09	3.58	2.70	Error	76	.237		
n	20	20	20	20					
				Breadth across the upper molars					
Mean	13.75	13.57	13.57	13.69	Area	1	.018	.10	.754
SD	.49	.56	.31	.26	Sex	1	.024	.13	.715
SE	.12	.12	.07	.06	A × S	1	.438	2.47	.120
CV	3.56	4.13	2.28	1.90	Error	76	.177		
n	20	20	20	20					

Table 21.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Breadth across the upper canines					
Mean	8.83	8.85	8.81	9.00	Area	1	.079	.66	.419
SD	.49	.31	.29	.26	Sex	1	.209	1.75	.190
SE	.12	.07	.06	.06	A × S	1	.129	1.08	.302
CV	5.55	3.50	3.29	2.89	Error	74	.119		
n	18	20	20	20					
				Length of the maxillary toothrow					
Mean	10.99	11.03	10.92	11.10	Area	1	.000	.00	.978
SD	.37	.33	.27	.29	Sex	1	.249	2.53	.116
SE	.09	.07	.06	.06	A × S	1	.101	1.02	.315
CV	3.37	2.99	2.47	2.61	Error	74	.098		
n	18	20	20	20					
				Length of the upper molariform toothrow					
Mean	9.03	9.07	8.95	9.11	Area	1	.009	.12	.731
SD	.30	.24	.30	.27	Sex	1	.170	2.21	.141
SE	.07	.05	.07	.06	A × S	1	.074	.96	.330
CV	3.32	2.65	3.35	2.96	Error	76	.077		
n	18	20	20	20					
				Width of the widest molar					
Mean	4.70	4.06	4.10	4.12	Area	1	.038	1.22	.272
SD	.18	.20	.17	.17	Sex	1	.000	.01	.917
SE	.04	.04	.04	.04	A × S	1	.002	.07	.787
CV	4.42	4.93	4.15	4.13	Error	74	.031		
n	18	20	20	20					
				Greatest length of the mandible					
Mean	21.60	21.66	21.10	21.48	Area	1	2.245	6.92	.010
SD	.44	.80	.44	.52	Sex	1	.968	2.98	.088
SE	.10	.18	.10	.12	A × S	1	.512	1.58	.213
CV	2.04	3.69	2.09	2.42	Error	76	.324		
n	20	20	20	20					
				Length of the mandibular toothrow					
Mean	12.19	12.22	11.98	12.32	Area	1	.069	.47	.495
SD	.33	.48	.40	.29	Sex	1	.670	4.58	.036
SE	.08	.11	.09	.06	A × S	1	.464	3.17	.079
CV	2.71	3.93	3.34	2.35	Error	76	.146		
n	18	20	20	20					
				Length of the coronoid process					
Mean	9.99	9.79	9.53	9.60	Area	1	2.113	11.06	.001
SD	.46	.50	.43	.34	Sex	1	.072	.38	.541
SE	.10	.11	.10	.08	A × S	1	.365	1.91	.171
CV	4.60	5.11	4.51	3.54	Error	76	.191		
n	20	20	20	20					

Numerous authors have published measurements of *D. rotundus* (see Swanepoel and Genoways, 1979) but only Cunha Vieira (1942) included Brazilian specimens. Individual variation was examined by Martinez and Villa-R (1940), however, the sexes were combined in their statistical analysis. Both Hershkovitz (1949) and Husson (1962) noted that males were smaller than females, but rigorous statistical analyses were not performed. Husson (1962) further suggested that differences among samples of *D. rotundus* from Suriname, Colombia, and Trinidad were not appreciable.

Table 22 summarizes the results of statistical analyses of individual, secondary sexual and geo-

Table 22.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Desmodus rotundus *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	77.85	80.95	78.60	81.00	Area	1	1.445	.09	.760
SD	3.70	3.99	3.36	4.62	Sex	1	68.306	4.45	.040
SE	.83	.89	1.50	1.75	A × S	1	1.106	.07	.790
CV	4.75	4.93	4.27	5.70	Error	48	15.348		
n	20	20	20	20					
Hindfoot length									
Mean	14.15	14.90	14.80	15.14	Area	1	1.800	3.60	.064
SD	.75	.64	.84	.69	Sex	1	2.697	5.39	.025
SE	.17	.14	.37	.26	A × S	1	.374	.75	.391
CV	5.30	4.30	5.68	4.56	Error	48	.500		
n	20	20	5	7					
Ear length									
Mean	17.45	18.15	18.00	18.29	Area	1	1.062	.68	.414
SD	1.47	.59	1.41	1.80	Sex	1	2.194	1.41	.242
SE	.33	.13	.63	.68	A × S	1	.388	.25	.621
CV	8.42	3.25	7.83	9.84	Error	48	1.561		
n	20	20	5	7					
Tragus length									
Mean	8.55	8.35	8.40	8.29	Area	1	.104	.21	.652
SD	.61	.59	.55	1.25	Sex	1	.223	.44	.509
SE	.14	.13	.25	.47	A × S	1	.017	.03	.857
CV	7.13	7.07	6.55	15.08	Error	48	.503		
n	20	20	5	7					
Forearm length									
Mean	60.30	63.55	60.60	65.57	Area	1	12.169	3.04	.088
SD	1.49	1.93	2.41	3.05	Sex	1	152.627	38.14	<.001
SE	.33	.43	1.08	1.15	A × S	1	6.691	1.67	.202
CV	2.47	3.04	3.98	4.65	Error	48	4.001		
n	20	20	5	7					
Weight									
Mean	39.78	44.58	43.50	47.43	Area	1	97.724	2.33	.133
SD	6.99	4.67	8.22	8.16	Sex	1	172.037	4.10	.048
SE	1.56	1.04	3.68	3.08	A × S	1	1.715	.04	.841
CV	17.57	10.48	18.90	17.20	Error	48	41.919		
n	20	20	5	7					
Length of digit one									
Mean	16.85	17.80	17.80	17.86	Area	1	2.290	1.68	.201
SD	1.18	1.01	1.48	1.35	Sex	1	2.290	1.68	.201
SE	.26	.23	.66	.51	A × S	1	1.800	1.32	.256
CV	7.00	5.67	8.31	7.56	Error	48	1.363		
n	20	20	5	7					
Length of digit three									
Mean	92.60	99.05	94.60	100.14	Area	1	21.600	1.11	.297
SD	4.84	3.87	4.39	4.60	Sex	1	324.774	16.69	<.001
SE	1.08	.87	1.97	1.74	A × S	1	1.858	.10	.759
CV	5.23	3.91	4.64	4.59	Error	48	19.454		
n	20	20	5	7					

Table 22.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit four									
Mean	75.80	80.50	76.40	81.71	Area	1	7.433	.85	.361
SD	2.63	3.00	2.70	3.82	Sex	1	226.452	25.95	<.001
SE	.59	.67	1.21	1.44	A × S	1	.852	.10	.756
CV	3.47	3.73	3.53	4.68	Error	48	8.726		
n	20	20	5	7					
Length of digit five									
Mean	73.65	78.85	75.20	79.29	Area	1	8.904	.95	.334
SD	2.16	2.91	3.42	5.06	Sex	1	194.701	20.80	<.001
SE	.48	.65	1.53	1.91	A × S	1	2.804	.30	.567
CV	2.93	3.69	4.55	6.38	Error	48	9.361		
n	20	20	5	7					
Tibia length									
Mean	27.90	29.35	29.00	30.71	Area	1	13.713	8.92	.004
SD	1.29	1.09	1.00	1.60	Sex	1	22.609	14.71	<.001
SE	.29	.24	.45	.61	A × S	1	.158	.10	.750
CV	4.62	3.71	3.45	5.21	Error	48	1.537		
n	20	20	5	7					
Greatest length of skull									
Mean	23.89	24.47	23.80	24.50	Area	1	.005	.02	.901
SD	.49	.65	.89	.28	Sex	1	3.511	10.31	.002
SE	.11	.15	.40	.11	A × S	1	.031	.09	.765
CV	2.05	2.66	3.74	1.14	Error	47	.341		
n	20	20	5	6					
Condylobasal length									
Mean	21.50	21.99	21.66	22.20	Area	1	.293	1.81	.185
SD	.43	.42	.37	.23	Sex	1	2.273	14.04	<.001
SE	.10	.09	.16	.09	A × S	1	.005	.03	.856
CV	2.00	1.91	1.71	1.04	Error	47	.162		
n	20	20	5	6					
Zygomatic breadth									
Mean	12.36	12.63	12.62	12.65	Area	1	.174	2.04	.160
SD	.28	.31	.19	.35	Sex	1	.187	2.19	.146
SE	.06	.07	.09	.14	A × S	1	.118	1.39	.245
CV	2.27	2.45	1.51	2.77	Error	47	.085		
n	20	20	5	6					
Postorbital constriction									
Mean	5.37	5.41	5.34	5.57	Area	1	.037	.72	.401
SD	.29	.28	.15	.25	Sex	1	.158	3.06	.087
SE	.06	.06	.07	.10	A × S	1	.071	1.37	.248
CV	5.40	5.18	2.81	4.49	Error	47	.052		
n	20	20	5	6					
Mastoid breadth									
Mean	12.73	12.84	12.76	12.90	Area	1	.017	.24	.627
SD	.29	.23	.15	.25	Sex	1	.134	1.85	.180
SE	.06	.06	.07	.10	A × S	1	.002	.03	.871
CV	2.28	2.18	1.18	1.94	Error	47	.072		
n	20	20	5	6					
Breadth of braincase									
Mean	12.44	12.49	12.60	12.55	Area	1	.109	2.15	.149
SD	.20	.27	.14	.12	Sex	1	.000	.00	.974
SE	.05	.06	.06	.05	A × S	1	.019	.38	.539
CV	1.61	2.16	1.11	.96	Error	47	.050		
n	20	20	5	6					

Table 22.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Rostral breadth									
Mean	7.83	7.97	7.62	7.73	Area	1	.418	4.65	.036
SD	.25	.34	.35	.29	Sex	1	.132	1.47	.232
SE	.06	.08	.16	.12	A × S	1	.001	.01	.916
CV	3.19	4.27	4.59	3.75	Error	47	.090		
n	20	20	5	6					
Height of braincase									
Mean	14.43	14.45	14.54	14.68	Area	1	.268	2.16	.149
SD	.37	.31	.11	.51	Sex	1	.057	.46	.501
SE	.08	.07	.05	.21	A × S	1	.033	.26	.611
CV	2.56	2.14	.76	3.47	Error	47	.124		
n	20	20	5	6					
Breadth across the upper molars									
Mean	6.74	6.93	6.76	6.67	Area	1	.122	1.47	.232
SD	.26	.31	.17	.37	Sex	1	.022	.27	.608
SE	.06	.07	.08	.15	A × S	1	.178	2.15	.149
CV	3.86	4.47	2.51	5.55	Error	47	.083		
n	20	20	5	6					
Breadth across the upper canines									
Mean	6.13	6.36	6.22	6.20	Area	1	.008	.21	.646
SD	.14	.20	.11	.32	Sex	1	.095	2.62	.112
SE	.03	.05	.05	.13	A × S	1	.134	3.71	.060
CV	2.28	3.14	1.77	5.16	Error	47	.036		
n	20	20	5	6					
Length of the maxillary toothrow									
Mean	3.42	3.32	3.42	3.43	Area	1	.030	1.81	.185
SD	.09	.18	.08	.05	Sex	1	.014	.86	.358
SE	.02	.04	.04	.02	A × S	1	.025	1.52	.224
CV	2.63	5.42	2.34	1.46	Error	47	.017		
n	20	20	5	6					
Length of the upper molariform toothrow									
Mean	1.33	1.31	1.36	1.40	Area	1	.033	3.37	.073
SD	.09	.11	.09	.11	Sex	1	.001	.13	.715
SE	.02	.02	.04	.05	A × S	1	.007	.65	.424
CV	6.77	8.40	6.62	7.86	Error	47	.010		
n	20	20	5	6					
Width of the widest molar									
Mean	.99	.92	.92	.98	Area	1	.000	.01	.926
SD	.11	.09	.11	.12	Sex	1	.000	.01	.926
SE	.03	.02	.05	.05	A × S	1	.038	3.54	.066
CV	11.11	9.78	11.96	12.24	Error	47	.011		
n	20	20	5	6					
Greatest length of the mandible									
Mean	15.06	15.49	15.50	15.67	Area	1	.802	5.56	.023
SD	.40	.38	.32	.35	Sex	1	.750	5.20	.027
SE	.09	.08	.15	.14	A × S	1	.143	.99	.324
CV	2.66	2.45	2.06	2.23	Error	47	.144		
n	20	20	5	6					
Length of the mandibular toothrow									
Mean	4.53	4.55	4.52	4.60	Area	1	.004	.12	.734
SD	.13	.22	.30	.13	Sex	1	.019	.52	.473
SE	.03	.05	.14	.05	A × S	1	.009	.24	.623
CV	2.87	4.84	6.64	2.83	Error	47	.037		
n	20	20	5	6					

Table 22.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of the coronoid process					
Mean	5.72	6.15	5.80	6.00	Area	1	.011	.08	.777
SD	.34	.41	.27	.28	Sex	1	.851	6.59	.014
SE	.08	.09	.12	.12	A × S	1	.113	.88	.353
CV	5.94	6.67	4.66	4.67	Error	47	.129		
n	20	20	5	6					

graphic variation in populations of *D. rotundus* from the Northeast of Brazil. In all but one case, female mean values are larger than male mean values and statistically significant secondary sexual variation is revealed for seven external and four cranial characters. The observations of sexual dimorphism by Husson (1962) and Hershkovitz (1949) are statistically corroborated. Cerrado sample means are larger than Caatingas sample means for 19 characters, three of which exhibit statistically significant variation. Caatingas specimens have larger sample means than Cerrado specimens for only one character and the difference is not statistically significant. The failure to achieve statistical significance for geographic variation is probably due to the small sample sizes from the Cerrado. However, the consistent direction of the difference between sample means from the Caatingas and Cerrado does suggest the strong possibility of geographic variation within the Northeast of Brazil.

Diphylla ecaudata Spix, 1823

Ojasti and Linares (1971) recognize two subspecies of this sanguinivore; *D. e. ecaudata* is the designation appropriate for specimens from the Northeast of Brazil. This species was rare in the Caatingas and apparently absent from the Chapada do Araripe.

Among the authors cited by Swanepoel and Genoways (1979) for contributing knowledge to *D. ecaudata*'s morphometric biology, only Dobson (1878), Lima (1926), and Cunha Vieira (1942) reported measurements from Brazilian specimens. Two adult males and two adult females were collected in the Caatingas; selected morphological measurements (after Swanepoel and Genoways, 1979) are herein reported (Total length: 70, 66, 74, 69; tail length: —, —, —, —; hindfoot length: 15, 13, 15, 12; ear length: 15, 14, 15, 14; greatest length of skull: 21.2, 20.8, 21.2, 21.1; condylobasal length: 18.9, 18.0, 19.0, 18.7; zygomatic breadth: 12.2, 11.6, 12.1, 11.7; postorbital constriction: 6.8, 6.2, 6.5, 6.5; length of the maxillary toothrow: 3.0, 2.9, 3.0, 2.9; and breadth across the upper molars: 5.2, 4.9, 5.0, 5.0). Caatingas specimens are on the average smaller than the group of specimens from North and Central America whose measurements are reported by Swanepoel and Genoways (1979).

Family Natalidae

Natalus stramineus Gray, 1838

This aerial insectivore was apparently absent from the Caatingas and rare on the Chapada do Araripe. Because only two adult male specimens were captured, only select measurements (after Swanepoel and Genoways, 1979) are reported here (total length: 99, 104; tail length: 53, 57; hindfoot length: 9, 8; ear length: 15, 12; greatest length of skull: —, 16.0; condylobasal length: —, 14.9; zygomatic breadth: —, 8.7; postorbital constriction: —, 3.2; breadth of braincase: —, —; length of the maxillary toothrow: —, 6.7; breadth across the upper molars: —, 4.0). Specimens from the Northeast should be included in the subspecies *N. s. natalensis* because they were captured within the defined range of that subspecies (Goodwin, 1959) and because morphometric comparison with the type specimen indicates correspondence.

Family Furipteridae

Furipterus horrens (F. Cuvier, 1828)

This poorly known aerial insectivore was rare in the Caatingas where it was only captured on serrotes. It was apparently absent from all habitats on the Chapada do Araripe. Only one adult male and one adult female specimen were captured, hence selected measurements (after Swanepoel and Genoways,

1979) only will be reported here (total length: 84, 80; tail length: 45, 44; hindfoot length: 6, 6; ear length: 10, 9; greatest length of skull: 12.0, 12.0; condylobasal length: 11.0, 11.0; zygomatic breadth: 7.2, 7.2; postorbital constriction: 2.9, 2.8; breadth of braincase: 5.6, 5.8; length of the maxillary toothrow: 4.3, 4.6; breadth across the upper molars: 4.5, 4.6). Uieda et al. (1980) summarize and present new data on aspects of the biology of *F. horrens*; unfortunately, little can be added from this study.

Family Vespertilionidae

Myotis nigricans (Schinz, 1821)

This aerial insectivore was rare to common in both Caatingas and Cerrado biomes. Of the three subspecies currently recognized, populations from the Northeast should tentatively be assigned to the subspecies *M. n. nigricans* (LaVal, 1973); however, further systematic analyses are required to substantiate morphometric homogeneity within the subspecies. The sexes occurred in statistically indistinguishable proportions in both Caatingas and Cerrado biomes (Binomial Test $P > .05$). Only 39% of the 41 captured adult specimens from the Chapada do Araripe were males while 44% of the 260 captured specimens from the Cerrado were males. *M. n. nigricans* were frequently found roosting under the roofing tiles of abandoned buildings throughout the Northeast; however, individuals were not found in aggregations of any size.

Myers (1978) detected statistical differences in forearm length between specimens of male and female *M. nigricans* from Paraguay. Williams and Findley (1979) found male sample means consistently smaller than female sample means for six mensural characters; however, only head and body length exhibited statistically significant variation. Table 23 summarizes the results of statistical analyses of individual, secondary sexual and geographic variation in populations of *M. nigricans* from the Northeast of Brazil. Statistically significant secondary sexual variation occurs only for a single variable, weight; further, a pattern in the relationship between male and female mean values is not apparent. *M. nigricans* populations from the Northeast of Brazil clearly do not exhibit sexual dimorphism in external and cranial characters.

Populations of *M. nigricans* from Caatingas and Cerrado biomes do not exhibit appreciable geographic variation either. Only two characters, calcar length and length from the canine to the last molar in the mandible, exhibit statistically significant variation between Caatingas and Cerrado sites; and trends in mean value relationships are not apparent. The Caatingas and Cerrado populations are morphometrically homogeneous.

Eptesicus furinalis D'Orbigny and Gervais, 1847

This aerial insectivore was apparently absent from the Caatingas and rare on the Chapada do Araripe. Williams (1978) suggested that Caatingas specimens of *E. furinalis* are most closely allied with the subspecies *E. f. chapmani*; however, the specimens he utilized were actually a subsample of the specimens caught in Cerrado habitats of the Chapada do Araripe.

Samples are small but sufficient for analyzing individual and secondary sexual variation by statistical methods; the results are summarized in Table 24. Females have larger sample means than males for ten external and 14 cranial characters. Males have larger sample means than females for five variables. Three of the characters (forearm length, weight, and greatest length of the maxillary) exhibited statistically significant secondary sexual variation; in all three cases, the male mean value was larger than the female mean value. Further, Williams (1978) suggested that sexual dimorphism existed in the Chapada population of *E. furinalis* based upon a multivariate analysis of variation.

Lasiurus borealis (Muller, 1776)

This aerial insectivore was rare on the Chapada do Araripe and apparently absent from the Caatingas. Its range extends from northern North America to southern South America.

Samples of *L. borealis* are small, but of sufficient size to attempt statistical analyses of individual and secondary sexual variation (Table 25). Females have larger sample means than males for all characters except postorbital constriction. Statistically significant secondary sexual variation was evidenced by four external and six cranial characters. Sexual dimorphism for size with females larger than males is strongly indicated by the data. This corroborates the findings of Williams and Findley (1979) which also indicated sexual dimorphism.

Lasiurus ega (Gervais, 1856)

This aerial insectivore was present but rare in both Caatingas and Cerrado biomes. According to the subspecies ranges suggested by Handley (1960), specimens from the Northeast of Brazil should be

Table 23.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Myotis nigricans *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	80.65	81.90	81.44	81.75	Area	1	1.912	.19	.661
SD	2.61	3.95	2.61	3.09	Sex	1	11.489	1.17	.283
SE	.58	.88	.65	.69	A × S	1	4.136	.42	.519
CV	3.24	4.82	3.20	3.78	Error	72	9.834		
n	20	20	16	20					
Tail length									
Mean	35.95	35.45	35.44	35.30	Area	1	2.065	.22	.641
SD	2.50	2.74	2.76	3.98	Sex	1	1.913	.20	.653
SE	.56	.61	.69	.89	A × S	1	.618	.07	.798
CV	6.95	7.73	7.79	11.27	Error	72	9.389		
n	20	20	16	20					
Hindfoot length									
Mean	5.95	6.00	5.94	5.90	Area	1	.060	.56	.458
SD	.39	0	.25	.45	Sex	1	.001	.01	.934
SE	.09	0	.06	.10	A × S	1	.036	.34	.563
CV	6.55	0	4.21	7.63	Error	72	.107		
n	20	20	16	20					
Ear length									
Mean	12.35	12.20	12.31	12.25	Area	1	.001	.00	.973
SD	.75	.77	.79	.85	Sex	1	.213	.34	.561
SE	.17	.17	.20	.19	A × S	1	.036	.06	.811
CV	6.07	6.31	6.42	6.94	Error	72	.624		
n	20	20	16	20					
Tragus length									
Mean	7.65	7.55	7.81	7.80	Area	1	.801	2.29	.134
SD	.59	.51	.54	.70	Sex	1	.060	.17	.681
SE	.13	.11	.14	.16	A × S	1	.036	.10	.749
CV	7.71	6.75	6.91	8.97	Error	72	.349		
n	20	20	16	20					
Forearm length									
Mean	34.40	33.85	34.00	33.80	Area	1	.953	.77	.382
SD	1.14	.88	1.32	1.11	Sex	1	2.647	2.15	.147
SE	.26	.20	.33	.25	A × S	1	.577	.47	.456
CV	3.31	2.60	3.88	3.28	Error	72	1.230		
n	20	20	16	20					
Weight									
Mean	4.50	4.95	4.34	4.88	Area	1	.252	.85	.359
SD	.46	.63	.44	.60	Sex	1	4.531	15.35	<.001
SE	.10	.14	.11	.14	A × S	1	.031	.11	.747
CV	10.22	12.73	10.14	12.30	Error	72	.295		
n	20	20	16	20					
Length of digit one									
Mean	4.95	4.70	4.63	4.70	Area	1	.497	1.70	.197
SD	.51	.47	.62	.57	Sex	1	.144	.49	.485
SE	.11	.11	.16	.13	A × S	1	.497	1.70	.197
CV	10.30	10.00	13.39	12.13	Error	72	.293		
n	20	20	16	20					

Table 23.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	56.50	56.65	56.06	56.60	Area	1	1.118	.16	.694
SD	2.91	2.23	2.59	2.91	Sex	1	2.224	.31	.580
SE	.65	.50	.65	.65	A × S	1	.707	.10	.755
CV	5.15	3.94	4.62	5.14	Error	72	7.185		
n	20	20	16	20					
Length of digit four									
Mean	47.45	47.10	45.88	47.30	Area	1	8.897	1.51	.223
SD	2.37	2.17	2.47	2.68	Sex	1	5.438	.92	.340
SE	.53	.49	.62	.60	A × S	1	14.827	2.51	.117
CV	4.99	4.61	5.38	5.67	Error	72	5.899		
n	20	20	16	20					
Length of digit five									
Mean	44.45	44.15	43.88	43.85	Area	1	3.603	.78	.381
SD	1.54	2.01	2.16	2.74	Sex	1	.497	.11	.744
SE	.34	.45	.54	.61	A × S	1	.356	.08	.783
CV	3.46	4.55	4.92	6.25	Error	72	.636		
n	20	20	16	20					
Tibia length									
Mean	15.45	15.00	15.19	15.20	Area	1	.018	.03	.869
SD	.95	.80	.75	.77	Sex	1	.901	1.33	.252
SE	.21	.18	.19	.17	A × S	1	1.007	1.49	.226
CV	6.15	5.33	4.94	5.07	Error	72	.675		
n	20	20	16	20					
Calcar length									
Mean	12.60	12.50	12.44	11.50	Area	1	6.360	3.99	.050
SD	1.27	1.47	1.26	1.00	Sex	1	5.065	3.18	.079
SE	.29	.33	.32	.22	A × S	1	3.301	2.07	.154
CV	10.08	11.76	10.13	8.70	Error	72	1.594		
n	20	20	16	20					
Greatest length of skull									
Mean	13.46	13.50	13.49	13.51	Area	1	.006	.06	.803
SD	.35	.29	.24	.30	Sex	1	.013	.14	.705
SE	.08	.07	.06	.07	A × S	1	.001	.01	.915
CV	2.60	2.15	1.78	2.22	Error	69	.092		
n	20	20	14	19					
Condylobasal length									
Mean	12.81	12.75	12.79	12.71	Area	1	.010	.11	.736
SD	.34	.24	.28	.29	Sex	1	.090	1.07	.305
SE	.08	.06	.08	.07	A × S	1	.002	.03	.872
CV	2.65	1.88	2.19	2.28	Error	69	.085		
n	20	20	14	19					
Zygomatic breadth									
Mean	8.26	8.30	8.36	8.32	Area	1	.054	1.67	.202
SD	.17	.16	.24	.18	Sex	1	.000	.00	.952
SE	.04	.04	.08	.05	A × S	1	.024	.73	.397
CV	2.06	1.93	2.87	2.16	Error	55	.032		
n	20	19	8	12					
Postorbital constriction									
Mean	3.29	3.25	3.29	3.25	Area	1	.000	.02	.878
SD	.09	.14	.12	.11	Sex	1	.028	2.11	.151
SE	.02	.03	.03	.02	A × S	1	.000	.02	.878
CV	2.74	4.31	3.65	3.38	Error	71	.013		
n	20	20	15	20					

Table 23.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Mastoid breadth				
Mean	6.94	6.93	6.93	6.92	Area	1	.002	.07	.794
SD	.12	.15	.10	.18	Sex	1	.002	.08	.777
SE	.03	.03	.03	.04	A × S	1	.000	.02	.887
CV	1.73	2.16	1.44	2.60	Error	68	.022		
n	20	20	13	19					
					Breadth of braincase				
Mean	6.48	6.40	6.38	6.42	Area	1	.029	1.09	.300
SD	.21	.13	.11	.17	Sex	1	.006	.24	.628
SE	.05	.03	.03	.04	A × S	1	.067	2.53	.116
CV	3.24	2.03	1.72	2.65	Error	69	.027		
n	20	20	14	19					
					Rostral breadth				
Mean	3.50	3.49	3.42	3.50	Area	1	.020	1.00	.322
SD	.11	.13	.13	.18	Sex	1	.020	1.00	.322
SE	.02	.03	.03	.04	A × S	1	.042	2.13	.149
CV	3.14	3.72	3.80	5.14	Error	71	.020		
n	20	20	15	20					
					Height of braincase				
Mean	6.67	6.70	6.59	6.58	Area	1	.168	3.61	.062
SD	.20	.20	.17	.26	Sex	1	.003	.06	.812
SE	.05	.05	.05	.06	A × S	1	.003	.06	.806
CV	3.00	2.99	2.58	3.95	Error	68	.046		
n	20	20	13	19					
					Breadth across the upper molars				
Mean	5.41	5.41	5.35	5.34	Area	1	.076	2.89	.094
SD	.18	.15	.17	.15	Sex	1	.001	.03	.854
SE	.04	.03	.05	.03	A × S	1	.000	.00	.956
CV	3.33	2.77	3.18	2.81	Error	68	.026		
n	20	20	13	19					
					Breadth across the upper canines				
Mean	3.42	3.48	3.46	3.48	Area	1	.008	.41	.526
SD	.15	.15	.10	.13	Sex	1	.024	1.30	.259
SE	.03	.03	.03	.03	A × S	1	.005	.27	.606
CV	4.39	4.31	2.89	3.74	Error	67	.019		
n	20	20	12	19					
					Length of the maxillary toothrow				
Mean	5.09	5.07	5.11	5.07	Area	1	.005	.28	.599
SD	.19	.11	.14	.10	Sex	1	.019	.98	.325
SE	.04	.02	.04	.02	A × S	1	.003	.14	.709
CV	3.73	2.17	2.74	1.97	Error	70	.019		
n	20	20	14	20					
					Length of the upper molariform toothrow				
Mean	4.22	4.21	4.16	4.22	Area	1	.010	.43	.512
SD	.20	.11	.18	.12	Sex	1	.015	.63	.429
SE	.04	.02	.05	.03	A × S	1	.021	.87	.354
CV	4.74	2.61	4.33	2.84	Error	70	.024		
n	20	20	14	20					
					Width of the widest molar				
Mean	1.58	1.56	1.58	1.57	Area	1	.001	.12	.726
SD	.06	.08	.11	.08	Sex	1	.003	.37	.543
SE	.01	.02	.03	.02	A × S	1	.000	.03	.868
CV	3.80	5.13	6.96	5.10	Error	70	.007		
n	20	20	14	20					

Table 23.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Greatest length of the mandible									
Mean	9.80	9.82	9.84	9.86	Area	1	.033	.44	.510
SD	.30	.26	.27	.27	Sex	1	.007	.10	.757
SE	.07	.06	.07	.06	A × S	1	.000	.00	.998
CV	3.06	2.65	2.74	2.74	Error	68	.075		
n	20	20	14	19					
Length of the mandibular toothrow									
Mean	5.55	5.55	5.43	5.43	Area	1	.279	7.75	.007
SD	.21	.15	.17	.22	Sex	1	.000	.00	.961
SE	.05	.03	.05	.05	A × S	1	.000	.00	.961
CV	3.78	2.70	3.13	4.05	Error	68	.036		
n	20	20	13	19					
Length of the coronoid process									
Mean	3.00	3.02	2.91	3.01	Area	1	.045	3.03	.086
SD	.14	.10	.10	.13	Sex	1	.055	3.73	.058
SE	.03	.02	.03	.03	A × S	1	.030	2.01	.161
CV	4.67	3.31	3.44	4.32	Error	67	.015		
n	20	20	13	18					

Table 24.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Eptesicus furinalis *males and females from the Cerrado biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean			96.71	97.40	Sex	1	2.244	.18	.678
SD			3.25	3.68	Within	20	12.651		
SE			1.23	.95					
CV			3.36	3.78					
n			7	15					
Tail length									
Mean			39.14	38.33	Sex	1	3.127	.38	.544
SD			1.35	3.31	Within	20	8.210		
SE			.51	.85					
CV			3.45	8.64					
n			7	15					
Hindfoot length									
Mean			7.00	6.33	Sex	1	2.121	2.77	.112
SD			.82	.90	Within	20	.767		
SE			.31	.23					
CV			11.71	14.22					
n			7	15					
Ear length									
Mean			13.57	13.67	Sex	1	.043	.07	.799
SD			.98	.72	Within	20	.652		
SE			.37	.19					
CV			7.22	5.27					
n			7	15					

Table 24.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Tragus length									
Mean			8.14	8.53	Sex	1	.728	1.00	.330
SD			.90	.83	Within	20	.730		
SE			.34	.22					
CV			11.06	8.73					
n			7	15					
Forearm length									
Mean			38.86	40.13	Sex	1	7.773	5.44	.030
SD			1.35	1.13	Within	20	1.430		
SE			.51	.29					
CV			3.47	2.82					
n			7	15					
Weight									
Mean			8.36	9.53	Sex	1	6.603	5.37	.031
SD			.69	1.25	Within	20	1.230		
SE			.26	.32					
CV			8.25	13.12					
n			7	15					
Length of digit one									
Mean			4.86	5.40	Sex	1	1.407	3.33	.083
SD			.69	.63	Within	20	.423		
SE			.26	.16					
CV			14.20	11.67					
n			7	15					
Length of digit three									
Mean			67.14	68.80	Sex	1	13.107	2.59	.123
SD			2.34	2.21	Within	20	5.063		
SE			.88	.57					
CV			3.48	3.21					
n			7	15					
Length of digit four									
Mean			55.86	57.07	Sex	1	6.982	2.50	.129
SD			1.68	1.67	Within	20	2.790		
SE			.63	.43					
CV			3.01	2.93					
n			7	15					
Length of digit five									
Mean			49.29	49.87	Sex	1	1.611	.75	.398
SD			1.38	1.51	Within	20	2.158		
SE			.52	.39					
CV			2.80	3.03					
n			7	15					
Tibia length									
Mean			16.00	16.27	Sex	1	.339	.30	.592
SD			0	1.28	Within	20	1.147		
SE			0	.33					
CV			0	7.87					
n			7	15					
Calcar length									
Mean			12.57	12.87	Sex	1	.416	.28	.601
SD			1.27	1.19	Within	20	1.472		
SE			.48	.30					
CV			10.10	9.25					
n			7	15					

Table 24.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Greatest length of skull									
Mean			14.88	14.84	Sex	1	.010	.11	.746
SD			.33	.28	Within	18	.088		
SE			.13	.08					
CV			2.22	1.89					
n			6	14					
Condylobasal length									
Mean			14.38	14.39	Sex	1	.000	.00	.993
SD			.28	.30	Within	17	.086		
SE			.11	.08					
CV			1.95	2.08					
n			6	13					
Zygomatic breadth									
Mean			10.52	10.56	Sex	1	.005	.08	.787
SD			.20	.30	Within	13	.072		
SE			.08	.10					
CV			1.90	2.84					
n			6	9					
Postorbital constriction									
Mean			3.59	3.64	Sex	1	.014	.56	.464
SD			.17	.16	Within	20	.025		
SE			.06	.04					
CV			4.74	4.40					
n			7	15					
Mastoid breadth									
Mean			8.25	8.35	Sex	1	.040	1.01	.327
SD			.15	.21	Within	19	.040		
SE			.06	.06					
CV			1.82	2.51					
n			6	15					
Breadth of braincase									
Mean			7.12	7.25	Sex	1	.080	3.57	.074
SD			.15	.15	Within	19	.022		
SE			.06	.04					
CV			2.11	2.07					
n			6	15					
Rostral breadth									
Mean			4.69	4.83	Sex	1	.104	2.31	.145
SD			.25	.19	Within	20	.045		
SE			.10	.05					
CV			5.33	3.93					
n			7	15					
Height of braincase									
Mean			7.42	7.47	Sex	1	.013	.18	.674
SD			.31	.24	Within	18	.069		
SE			.13	.07					
CV			4.18	3.21					
n			6	14					
Breadth across the upper molars									
Mean			6.46	6.51	Sex	1	.015	.46	.505
SD			.10	.21	Within	20	.033		
SE			.04	.05					
CV			1.55	3.23					
n			7	15					

Table 24.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Breadth across the upper canines					
Mean			4.61	4.80	Sex	1	.161	2.30	.146
SD			.20	.29	Within	19	.070		
SE			.07	.08					
CV			4.34	6.04					
n			7	14					
				Length of the maxillary toothrow					
Mean			5.63	5.65	Sex	1	.003	.06	.810
SD			.10	.19	Within	20	.028		
SE			.04	.05					
CV			1.78	3.36					
n			7	15					
				Length of the upper molariform toothrow					
Mean			4.53	4.51	Sex	1	.001	.06	.810
SD			.15	.13	Within	20	.019		
SE			.06	.03					
CV			3.31	2.88					
n			7	15					
				Width of the widest molar					
Mean			1.94	2.00	Sex	1	.016	2.27	.147
SD			.08	.09	Within	20	.007		
SE			.03	.02					
CV			2.29	4.50					
n			7	15					
				Greatest length of the mandible					
Mean			11.43	11.79	Sex	1	.635	9.05	.007
SD			.16	.30	Within	20	.070		
SE			.06	.08					
CV			1.40	2.54					
n			7	15					
				Length of the mandibular toothrow					
Mean			6.13	6.20	Sex	1	.024	.66	.425
SD			.18	.20	Within	20	.037		
SE			.07	.05					
CV			2.94	3.23					
n			7	15					
				Length of the coronoid process					
Mean			4.39	4.42	Sex	1	.006	.19	.668
SD			.17	.17	Within	20	.030		
SE			.06	.05					
CV			3.87	3.85					
n			7	15					

considered *L. e. argentinus.* However, he should have used the appellation *L. e. caudatus* (based upon a specimen from Pernambuco) which he puts in synonymy with *L. e. argentinus,* though it (*caudatus*) is the older name (Koopman, in litt.).

The morphometric data are pooled from the Caatingas and Cerrado biomes because the samples from each area alone are too small to perform statistical analyses. Table 26 summarizes the results of a statistical analysis of individual and secondary sexual variation in pooled samples. Only a single variable, forearm length, exhibits statistically significant secondary sexual variation. Females tended to have larger sample means than males, especially for ex-

Table 25.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Lasiurus borealis *males and females from the Cerrado biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean			99.67	105.53	Sex	1	64.222	2.78	.140
SD			3.98	6.43	Within	7	23.143		
SE			1.63	3.71					
CV			3.99	6.10					
n			6	3					
				Tail length					
Mean			41.00	46.00	Sex	1	50.000	7.29	.031
SD			2.90	1.73	Within	7	6.857		
SE			1.18	1.00					
CV			7.07	3.76					
n			6	3					
				Hindfoot length					
Mean			7.33	7.67	Sex	1	.222	.78	.407
SD			.52	.58	Within	7	.286		
SE			.21	.33					
CV			7.09	7.56					
n			6	3					
				Ear length					
Mean			10.17	10.67	Sex	1	.500	2.33	.171
SD			.41	.58	Within	7	.214		
SE			.17	.33					
CV			4.03	5.44					
n			6	3					
				Tragus length					
Mean			6.00	6.67	Sex	1	.889	2.33	.171
SD			.63	.58	Within	7	.381		
SE			.26	.33					
CV			10.50	8.70					
n			6	3					
				Forearm length					
Mean			38.83	40.67	Sex	1	6.722	4.09	.083
SD			1.17	1.53	Within	7	1.643		
SE			.48	.88					
CV			3.01	3.76					
n			6	3					
				Weight					
Mean			8.00	8.43	Sex	1	1.389	8.33	.023
SD			.45	.29	Within	7	.167		
SE			.18	.17					
CV			5.63	3.44					
n			6	3					
				Length of digit one					
Mean			8.50	9.33	Sex	1	1.389	4.49	.072
SD			.55	.58	Within	7	.310		
SE			.22	.33					
CV			6.47	6.22					
n			6	3					

Table 25.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Length of digit three					
Mean			77.17	82.67	Sex	1	60.500	5.07	.059
SD			2.93	4.51	Within	7	11.929		
SE			1.20	2.60					
CV			3.80	5.46					
n			6	3					
				Length of digit four					
Mean			59.00	64.67	Sex	1	64.222	15.68	.006
SD			2.37	.58	Within	7	4.095		
SE			.07	.33					
CV			4.02	.90					
n			6	3					
				Length of digit five					
Mean			50.33	53.33	Sex	1	18.000	.86	.384
SD			5.35	1.15	Within	7	20.857		
SE			2.19	.67					
CV			10.63	2.16					
n			6	3					
				Tibia length					
Mean			19.67	21.00	Sex	1	3.556	7.47	.029
SD			.82	0	Within	7	.476		
SE			.33	0					
CV			4.17	0					
n			6	3					
				Calcar length					
Mean			13.17	13.33	Sex	1	.056	.03	.879
SD			1.17	2.08	Within	7	2.214		
SE			.48	1.20					
CV			8.88	15.60					
n			6	3					
				Greatest length of skull					
Mean			11.27	11.70	Sex	1	.376	4.59	.070
SD			.08	.52	Within	7	.082		
SE			.03	.30					
CV			.71	4.44					
n			6	3					
				Condylobasal length					
Mean			10.87	11.33	Sex	1	.436	5.44	.052
SD			.16	.46	Within	7	.080		
SE			.07	.27					
CV			1.47	4.06					
n			6	3					
				Zygomatic breadth					
Mean			8.53	8.80	Sex	1	.142	7.47	.029
SD			.10	.20	Within	7	.019		
SE			.04	.12					
CV			1.17	2.27					
n			6	3					
				Postorbital constriction					
Mean			4.23	4.17	Sex	1	.009	.62	.456
SD			.10	.15	Within	7	.014		
SE			.04	.09					
CV			2.36	3.60					
n			6	3					

Table 25.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Mastoid breadth									
Mean			7.20	7.47	Sex	1	.142	6.79	.035
SD			.16	.12	Within	7	.021		
SE			.06	.07					
CV			2.22	1.61					
n			6	3					
Breadth of braincase									
Mean			6.97	7.07	Sex	1	.020	.87	.381
SD			.10	.23	Within	7	.023		
SE			.04	.13					
CV			1.43	3.25					
n			6	3					
Rostral breadth									
Mean			4.48	4.77	Sex	1	.161	4.41	.074
SD			.16	.25	Within	7	.036		
SE			.07	.15					
CV			3.57	5.24					
n			6	3					
Height of braincase									
Mean			8.12	8.13	Sex	1	.001	.01	.924
SD			.27	.12	Within	7	.056		
SE			.11	.07					
CV			3.33	1.48					
n			6	3					
Breadth across the upper molars									
Mean			5.27	5.70	Sex	1	.376	11.27	.012
SD			.21	.10	Within	7	.033		
SE			.08	.06					
CV			3.98	1.75					
n			6	3					
Breadth across the upper canines									
Mean			4.35	4.87	Sex	1	.534	30.72	<.001
SD			.15	.06	Within	7	.017		
SE			.06	.03					
CV			3.45	1.23					
n			6	3					
Length of the maxillary toothrow									
Mean			3.82	4.00	Sex	1	.067	4.34	.076
SD			.08	.20	Within	7	.016		
SE			.03	.12					
CV			2.09	5.00					
n			6	3					
Length of the upper molariform toothrow									
Mean			3.13	3.13	Sex	1	.000	.00	1.000
SD			.10	.15	Within	7	.014		
SE			.04	.08					
CV			3.19	4.79					
n			6	3					
Width of the widest molar									
Mean			1.38	1.40	Sex	1	.001	.08	.785
SD			.10	0	Within	7	.007		
SE			.04	0					
CV			7.25	0					
n			6	3					

Table 25.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Greatest length of the mandible					
Mean			8.45	8.93	Sex	1	.467	32.17	<.001
SD			.12	.11	Within	7	.015		
SE			.05	.07					
CV			1.42	1.23					
n			6	3					
				Length of the mandibular toothrow					
Mean			4.47	4.70	Sex	1	.109	6.73	.036
SD			.10	.17	Within	7	.016		
SE			.04	.10					
CV			2.24	3.62					
n			6	3					
				Length of the coronoid process					
Mean			2.65	2.80	Sex	1	.045	4.20	.080
SD			.11	.10	Within	7	.011		
SE			.04	.06					
CV			4.15	3.57					
n			6	3					

Table 26.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Lasiurus ega *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (*$P < .050$*) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Total length					
Mean	121.50	122.50	120.00	134.00	Sex	1	27.075	1.19	.318
SD	2.12	2.89	—	—	Within	6	22.800		
SE	1.50	1.44	—	—					
CV	1.75	2.36	—	—					
n	2	4	1	1					
				Tail length					
Mean	57.00	52.50	50.00	52.00	Sex	1	9.633	.80	.404
SD	4.24	2.65	—	—	Within	6	11.978		
SE	3.00	1.32	—	—					
CV	7.44	5.05	—	—					
n	2	4	1	1					
				Hindfoot length					
Mean	8.00	7.00	8.00	8.00	Sex	1	1.200	2.57	.160
SD	0	.82	—	—	Within	6	.467		
SE	0	.41	—	—					
CV	0	11.71	—	—					
n	2	4	1	1					
				Ear length					
Mean	15.50	16.75	16.00	15.00	Sex	1	1.008	.28	.618
SD	2.12	2.22	—	—	Within	6	3.644		
SE	1.50	1.10	—	—					
CV	13.68	13.25	—	—					
n	2	4	1	1					

Table 26.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Tragus length									
Mean	9.50	9.75	10.00	9.00	Sex	1	.008	.03	.875
SD	.71	.50	—	—	Within	6	.311		
SE	.50	.25	—	—					
CV	7.47	5.13	—	—					
n	2	4	1	1					
Forearm length									
Mean	46.50	48.50	44.00	49.00	Sex	1	16.133	6.10	.049
SD	.71	1.92	—	—	Within	6	2.644		
SE	.50	.96	—	—					
CV	1.53	3.96	—	—					
n	2	4	1	1					
Weight									
Mean	13.75	15.00	13.00	14.50	Sex	1	3.675	.61	.465
SD	1.06	3.39	—	—	Within	6	6.033		
SE	.75	1.70	—	—					
CV	7.71	22.60	—	—					
n	2	4	1	1					
Length of digit one									
Mean	8.00	8.00	8.00	9.00	Sex	1	.075	.16	.702
SD	0	.82	—	—	Within	6	.467		
SE	0	.41	—	—					
CV	0	10.25	—	—					
n	2	4	1	1					
Length of digit three									
Mean	90.00	90.50	86.00	91.00	Sex	1	7.008	1.32	.294
SD	2.83	1.08	—	—	Within	6	5.311		
SE	2.00	1.04	—	—					
CV	3.14	2.99	—	—					
n	2	4	1	1					
Length of digit four									
Mean	70.00	71.25	67.00	71.00	Sex	1	9.075	3.68	.104
SD	1.41	1.50	—	—	Within	6	2.467		
SE	1.00	.75	—	—					
CV	2.01	2.11	—	—					
n	2	4	1	1					
Length of digit five									
Mean	57.50	58.00	55.00	58.00	Sex	1	3.333	1.87	.220
SD	.71	1.41	—	—	Within	6	1.778		
SE	.50	.71	—	—					
CV	1.23	2.43	—	—					
n	2	4	1	1					
Tibia length									
Mean	21.50	21.25	21.00	22.00	Sex	1	.008	.03	.875
SD	.71	.50	—	—	Within	6	.311		
SE	.50	.25	—	—					
CV	3.30	2.35	—	—					
n	2	4	1	1					
Calcar length									
Mean	17.00	17.25	18.00	19.00	Sex	1	.133	.05	.830
SD	2.83	1.26	—	—	Within	6	2.644		
SE	2.00	.63	—	—					
CV	16.65	7.30	—	—					
n	2	4	1	1					

Table 26.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
				Greatest length of skull					
Mean	15.00	15.13	14.90	15.50	Sex	1	.114	1.26	.313
SD	.57	.11	—	—	Within	5	.091		
SE	.40	.07	—	—					
CV	3.80	.73	—	—					
n	2	3	1	1					
				Condylobasal length					
Mean	14.50	14.80	14.50	15.00	Sex	1	.210	4.57	.086
SD	.42	.10	—	—	Within	5	.046		
SE	.30	.06	—	—					
CV	2.90	.68	—	—					
n	2	3	1	1					
				Zygomatic breadth					
Mean	10.55	10.83	10.60	10.80	Sex	1	.114	1.62	.260
SD	.07	.42	—	—	Within	5	.071		
SE	.05	.24	—	—					
CV	.66	3.88	—	—					
n	2	3	1	1					
				Postorbital constriction					
Mean	4.75	4.58	4.60	4.30	Sex	1	.061	.47	.517
SD	.21	.47	—	—	Within	6	.128		
SE	.15	.23	—	—					
CV	4.42	10.26	—	—					
n	2	4	1	1					
				Mastoid breadth					
Mean	8.75	8.90	8.70	8.60	Sex	1	.014	.41	.549
SD	.21	.17	—	—	Within	5	.035		
SE	.15	.10	—	—					
CV	2.42	1.91	—	—					
n	2	4	1	1					
				Breadth of braincase					
Mean	8.20	8.23	8.40	8.10	Sex	1	.008	.09	.772
SD	.42	.31	—	—	Within	5	.081		
SE	.30	.18	—	—					
CV	5.12	3.77	—	—					
n	2	4	1	1					
				Rostral breadth					
Mean	5.85	5.30	5.90	6.00	Sex	1	.263	1.14	.335
SD	.07	.62	—	—	Within	5	.231		
SE	.05	.36	—	—					
CV	1.20	11.70	—	—					
n	2	3	1	1					
				Height of braincase					
Mean	8.95	8.90	9.20	8.80	Sex	1	.043	1.23	.317
SD	.21	.20	—	—	Within	5	.035		
SE	.15	.12	—	—					
CV	2.35	2.25	—	—					
n	2	3	1	1					
				Breadth across the upper molars					
Mean	7.10	6.88	6.90	7.30	Sex	1	.010	.15	.710
SD	.14	.26	—	—	Within	6	.066		
SE	.10	.13	—	—					
CV	1.97	3.78	—	—					
n	2	4	1	1					

Table 26.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Breadth across the upper canines									
Mean	5.90	5.83	6.10	5.90	Sex	1	.023	.54	.496
SD	.14	.29	—	—	Within	5	.043		
SE	.10	.17	—	—					
CV	2.37	4.97	—	—					
n	2	3	1	1					
Length of the maxillary toothrow									
Mean	5.35	5.37	5.30	5.50	Sex	1	.008	.57	.484
SD	.07	.15	—	—	Within	5	.013		
SE	.05	.09	—	—					
CV	1.31	2.79	—	—					
n	2	3	1	1					
Length of the upper molariform toothrow									
Mean	4.15	4.27	4.20	4.50	Sex	1	.043	3.97	.103
SD	.07	.06	—	—	Within	5	.011		
SE	.05	.03	—	—					
CV	1.69	1.41	—	—					
n	2	3	1	1					
Width of the widest molar									
Mean	2.00	2.08	2.00	2.30	Sex	1	.027	2.38	.174
SD	0	.10	—	—	Within	6	.011		
SE	0	.05	—	—					
CV	0	4.81	—	—					
n	2	4	1	1					
Greatest length of the mandible									
Mean	11.10	11.63	11.30	10.60	Sex	1	.120	.77	.413
SD	.14	.13	—	—	Within	6	.156		
SE	.10	.06	—	—					
CV	1.26	1.11	—	—					
n	2	4	1	1					
Length of the mandibular toothrow									
Mean	6.15	6.20	6.20	5.80	Sex	1	.008	.14	.721
SD	.07	.27	—	—	Within	5	.053		
SE	.05	.15	—	—					
CV	1.13	4.35	—	—					
n	2	3	1	1					
Length of the coronoid process									
Mean	4.00	3.90	4.00	4.60	Sex	1	.003	.03	.865
SD	0	.25	—	—	Within	6	.095		
SE	0	.12	—	—					
CV	0	6.41	—	—					
n	2	4	1	1					

ternal characteristics, but the relationship between male and female sample means was not consistent enough to suggest the existence of sexual dimorphism in this species.

Family Molossidae

Molossops planirostris (Peters, 1865)

This fast-flying aerial insectivore was rare in the Caatingas and apparently absent from the Chapada do Araripe. The subspecific status of populations from the Northeast is uncertain. The three captured specimens were obtained from a hollow in a cut tree from Caatinga Alta.

Vizotto and Taddei (1976) statistically analyzed individual and secondary sexual variation in *M. planirostris.* They showed conclusively that males are larger than females on the average and that statistically significant secondary sexual variation occurs for most external and all cranial characters analyzed.

The three individuals captured from the Caatingas do not constitute a sufficiently large sample for statistical analyses so only selected measurements (after Swanepoel and Genoways, 1979) are presented here for an adult male and two adult female specimens (total length: 96, 93, 92; tail length: 22, 24, 26; hindfoot length: 5, 6, 6; ear length: 16, 17, 14; greatest length of skull: 16.1, 15.1, 15.4; condylobasal length: 15.8, 15.0, 14.9; zygomatic breadth: 11.2, 10.8, 11.0; postorbital constriction: 4.3, 4.1, 4.2; breadth of braincase: 7.8, 7.5, 7.8; length of the maxillary toothrow: 6.5, 6.3, 6.0; breadth across the upper molars: 7.7, 7.7, 7.7).

Molossops temminckii (Burmeister, 1854)

This molossid aerial insectivore was rare in the Caatingas and on the Chapada do Araripe. Based upon coloration characteristics and the distributional information summarized by Vizotto and Taddei (1976), specimens from northeastern Brazil should be considered *M. t. temminckii.*

Vizotto and Taddei (1976) are the only authors to analyze morphometric relations in *M. temminckii* via statistical techniques. None of the 17 external characters they examine exhibit statistically significant secondary sexual variation, and consistent mean value relations between males and females are not evident. On the other hand, males are consistently larger than females for cranial characters, but only two characters exhibit statistically significant differences.

In order to perform statistical analyses of individual and secondary sexual variation for specimens from the Northeast of Brazil, samples are combined from Caatingas and Cerrado biomes; the results of the analyses are summarized in Table 27. None of the external or cranial characters exhibit statistically significant secondary sexual variation, however, male sample means are consistently larger than those of females. Although data from the Northeast as well as that of Vizotto and Taddei (1976) fail to detect significant differences between males and females, both analyses strongly suggest sexual dimorphism with males larger than females, at least for cranial characters. Larger sample sizes or a multivariate analysis of variance would facilitate the detection of sexual dimorphism in this species.

Tadarida laticaudata (E. Geoffroy, 1805)

This fast-flying aerial insectivore was rare in the Caatingas and on the Chapada do Araripe. Samples from the Northeast of Brazil are small, so selected measurements (after Swanepoel and Genoways, 1979) of an adult male and female from the Caatingas and an adult male from the Chapada do Araripe are herein reported (total length: 96, 96, 107; tail length: 37, 39, 36; hindfoot length: 8, 8, 8; ear length: 18, 18, 20; greatest length of skull: 15.7, 16.2, —; condylobasal length: 14.9, 15.2, —; zygomatic breadth: 9.3, 9.3, —; postorbital constriction: 3.3, 3.2, —; breadth of braincase: 8.0, 7.7, —; length of the maxillary toothrow: 6.1, 6.2, —; and breadth across the upper molars: 6.6, 6.6, —).

Neoplatymops mattogrossensis (Cunha Vieira, 1942)

This small molossid aerial insectivore was common in rocky habitats and on serrotes in the Caatingas where it roosted in low-lying rock crevices. Approximately 46% of the 48 captured adult specimens from the Caatingas were males; as such, the sexes occurred in statistically indistinguishable proportions (Binomial Test, $P > .05$). *N. mattogrossensis* is absent from the Chapada do Araripe.

The biology of this species is poorly known. Other than the original description (Cunha Vieira, 1942) and the revision of flat-headed bats by Peterson (1965), only isolated distributional records appear in the literature (Handley, 1976; Sazima and Taddei, 1976). In a multivariate analysis of the family Molossidae, Freeman (1981) recently suggested allocating specimens in this species to the genus *Molossops*; however a consensus on this taxonomic question is not yet apparent. Both Peterson (1965) and Sazima and Taddei (1976) report mensural data for *N. mattogrossensis* but no one has statistically examined individual or secondary sexual variation in this species. Willig (unpublished ms.) has detected statistically significant geographic variation within and among populations of *Neoplatymops* from the Northeast of Brazil, southern Venezuela, and southwestern British Guiana.

Table 28 summarizes the results of a statistical analysis of individual and secondary sexual variation in this species. Like other molossids, *Neoplatymops* exhibits appreciable sexual dimorphism. Males have larger sample means than females for 12 of the 13 external characters. Males have larger sample means than females for all 16 cranial char-

Table 27.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Molossops temminckii *males and females from both Caatinga and Cerrado biomes. Due to small sample sizes, data from both biomes were combined to determine the existence of significant (P < .050) secondary sexual variation via a one-way analysis of variance (Model I) with replication.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	78.00	82.67	79.25	81.33	Sex	1	24.55	2.83	.127
SD	—	3.22	2.50	4.16	Within	9	8.67		
SE	—	1.86	1.25	2.40					
CV	—	3.90	3.15	5.11					
n	1	3	4	3					
Tail length									
Mean	21.00	24.00	26.00	29.00	Sex	1	6.136	.43	.510
SD	—	3.46	3.74	1.72	Within	9	14.389		
SE	—	2.00	1.87	1.00					
CV	—	14.42	14.38	5.97					
n	1	3	4	3					
Hindfoot length									
Mean	6.00	5.00	5.25	5.00	Sex	1	.436	.55	.479
SD	—	1.00	.96	1.00	Within	9	.800		
SE	—	.48	.48	.58					
CV	—	20.00	18.29	20.00					
n	1	3	4	3					
Ear length									
Mean	12.00	12.67	13.00	12.33	Sex	1	.246	.51	.492
SD	—	.58	.82	.58	Within	9	.478		
SE	—	.33	.41	.33					
CV	—	4.58	6.31	4.70					
n	1	3	4	3					
Tragus length									
Mean	3.00	2.67	2.25	3.33	Sex	1	.982	1.23	.297
SD	—	.58	.50	1.53	Within	9	.800		
SE	—	.33	.25	.88					
CV	—	21.72	22.22	45.94					
n	1	3	4	3					
Forearm length									
Mean	33.00	31.67	31.50	31.00	Sex	1	.594	.87	.375
SD	—	.58	.58	1.00	Within	9	.682		
SE	—	.33	.29	.58					
CV	—	1.83	1.84	3.23					
n	1	3	4	3					
Weight									
Mean	6.50	7.00	6.88	6.33	Sex	1	.049	.08	.787
SD	—	.50	1.03	.76	Within	9	.626		
SE	—	.29	.52	.44					
CV	—	7.14	14.97	12.01					
n	1	3	4	3					
Length of digit one									
Mean	5.00	4.33	4.75	4.67	Sex	1	.246	.96	.353
SD	—	.58	.50	.58	Within	9	.256		
SE	—	.33	.25	.33					
CV	—	13.39	10.53	12.42					
n	1	3	4	3					

Table 27.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	62.00	61.33	60.50	61.00	Sex	1	.367	.02	.880
SD	—	1.53	6.56	1.00	Within	9	15.293		
SE	—	.88	3.28	.58					
CV	—	2.49	10.84	1.64					
n	1	3	4	3					
Length of digit four									
Mean	52.00	51.00	51.50	51.00	Sex	1	.982	.32	.524
SD	—	1.73	2.52	1.00	Within	9	3.022		
SE	—	1.00	1.26	.58					
CV	—	3.39	4.89	1.96					
n	1	3	4	3					
Length of digit five									
Mean	38.00	35.67	36.50	35.67	Sex	1	3.503	1.42	.263
SD	—	1.53	1.92	1.53	Within	9	2.459		
SE	—	.88	.96	.80					
CV	—	4.29	5.26	4.29					
n	1	3	4	3					
Tibia length									
Mean	11.00	10.00	10.50	10.33	Sex	1	.512	2.27	.166
SD	—	0	.58	.58	Within	9	.226		
SE	—	0	.29	.33					
CV	—	0	5.52	5.61					
n	1	3	4	3					
Calcar length									
Mean	10.00	10.33	9.25	8.34	Sex	1	.012	.01	.941
SD	—	1.16	1.26	1.53	Within	9	2.059		
SE	—	.67	.63	.88					
CV	—	11.23	13.62	18.35					
n	1	3	4	3					
Greatest length of skull									
Mean	13.20	13.23	13.43	13.20	Sex	1	.060	.54	.485
SD	—	.31	.45	.36	Within	8	.112		
SE	—	.18	.26	.21					
CV	—	2.34	3.35	2.73					
n	1	3	3	3					
Condylobasal length									
Mean	13.10	13.10	13.10	12.83	Sex	1	.043	.24	.634
SD	—	.27	.66	.38	Within	8	.174		
SE	—	.15	.38	.22					
CV	—	2.06	5.04	2.96					
n	1	3	3	3					
Zygomatic breadth									
Mean	9.00	9.27	9.40	9.20	Sex	1	.008	.08	.784
SD	—	.06	.53	0	Within	7	.099		
SE	—	.03	.31	0					
CV	—	.65	5.64	0					
n	1	3	3	2					
Postorbital constriction									
Mean	3.70	3.67	3.70	3.70	Sex	1	.001	.06	.812
SD	—	.06	.10	.17	Within	8	.011		
SE	—	.03	.06	.10					
CV	—	1.63	2.70	4.59					
n	1	3	3	3					

Table 27.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Mastoid breadth				
Mean	8.80	8.67	8.90	8.40	Sex	1	.280	2.20	.177
SD	—	.15	.62	.20	Within	8	.128		
SE	—	.09	.36	.11					
CV	—	1.73	6.97	2.38					
n	1	3	3	3					
					Breadth of braincase				
Mean	6.90	7.13	7.17	7.17	Sex	1	.006	.12	.736
SD	—	.15	.32	.21	Within	8	.049		
SE	—	.09	.19	.12					
CV	—	2.10	4.46	2.93					
n	1	3	3	3					
					Rostral breadth				
Mean	5.10	5.20	5.03	4.90	Sex	1	.000	.00	1.000
SD	—	0	.21	.17	Within	8	.036		
SE	—	0	.12	.10					
CV	—	0	4.17	3.47					
n	1	3	3	3					
					Height of braincase				
Mean	6.50	6.83	7.17	6.67	Sex	1	.150	.68	.432
SD	—	.31	.61	.47	Within	8	.219		
SE	—	.18	.35	.27					
CV	—	4.54	8.51	7.05					
n	1	3	3	3					
					Breadth across the upper molars				
Mean	6.60	6.47	6.73	6.70	Sex	1	.033	.44	.524
SD	—	.15	.46	.10	Within	8	.074		
SE	—	.09	.27	.06					
CV	—	2.32	6.84	1.49					
n	1	3	3	3					
					Breadth across the upper canines				
Mean	3.70	3.83	4.00	3.73	Sex	1	.048	1.63	.237
SD	—	.06	.17	.21	Within	8	.030		
SE	—	.03	.10	.12					
CV	—	1.57	4.25	5.63					
n	1	3	3	3					
					Length of the maxillary toothrow				
Mean	5.50	5.13	5.17	5.20	Sex	1	.017	.73	.419
SD	—	.15	.15	0	Within	8	.030		
SE	—	.09	.09	0					
CV	—	2.92	2.90	0					
n	1	3	3	3					
					Length of the upper molariform toothrow				
Mean	4.50	4.40	4.33	4.33	Sex	1	.000	.02	.886
SD	—	.10	.06	.06	Within	8	.008		
SE	—	.06	.03	.03					
CV	—	2.27	1.39	1.39					
n	1	3	3	3					
					Width of the widest molar				
Mean	2.00	1.93	1.80	1.80	Sex	1	.001	.05	.826
SD	—	.06	.10	.10	Within	8	.013		
SE	—	.03	.06	.06					
CV	—	3.11	5.56	5.56					
n	1	3	3	3					

Table 27.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Greatest length of the mandible									
Mean	10.50	10.40	10.37	10.30	Sex	1	.006	.09	.776
SD	—	.36	.32	.17	Within	8	.069		
SE	—	.21	.19	.10					
CV	—	3.46	3.09	1.65					
n	1	3	3	3					
Length of the mandibular toothrow									
Mean	5.90	5.80	5.93	5.80	Sex	1	.038	1.12	.321
SD	—	0	.25	.27	Within	8	.033		
SE	—	0	.15	.15					
CV	—	0	4.22	4.66					
n	1	3	3	3					
Length of the coronoid process									
Mean	3.40	3.20	3.20	3.20	Sex	1	.006	.15	.713
SD	—	.10	.36	.20	Within	8	.041		
SE	—	.06	.21	.06					
CV	—	3.13	11.25	3.13					
n	1	3	3	3					

Table 28.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Neoplatymops mattogrossensis *males and females from the Caatinga biome. A one-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	79.14	76.81			Sex	1	64.621	4.19	.046
SD	3.12	4.49			Within	46	15.405		
SE	.67	.88							
CV	3.94	5.85							
n	22	26							
Tail length									
Mean	25.50	25.65			Sex	1	.282	.04	.843
SD	2.84	2.50			Within	46	7.074		
SE	.61	.49							
CV	11.14	9.75							
n	22	26							
Hindfoot length									
Mean	5.27	4.96			Sex	1	1.154	4.70	.040
SD	.55	.45			Within	46	.246		
SE	.12	.09							
CV	10.44	9.07							
n	22	26							
Ear length									
Mean	13.36	13.12			Sex	1	.734	1.71	.197
SD	.58	.71			Within	46	.429		
SE	.12	.14							
CV	4.34	4.51							
n	22	26							

Table 28.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Tragus length									
Mean	3.14	3.04			Sex	1	.114	.21	.650
SD	.89	.60			Within	46	.556		
SE	.19	.12							
CV	28.34	19.74							
n	22	26							
Forearm length									
Mean	30.05	30.23			Sex	1	.409	.43	.514
SD	.90	1.03			Within	46	.947		
SE	.19	.20							
CV	3.00	3.41							
n	22	26							
Weight									
Mean	6.11	5.39			Sex	1	6.333	8.42	.006
SD	.64	1.02			Within	46	.753		
SE	.14	.20							
CV	10.47	18.92							
n	22	26							
Length of digit one									
Mean	5.54	5.16			Sex	1	1.739	3.15	.083
SD	.60	.85			Within	45	.551		
SE	.13	.17							
CV	10.83	16.47							
n	22	25							
Length of digit three									
Mean	55.22	54.16			Sex	1	13.330	6.30	.016
SD	1.11	1.70			Within	45	2.116		
SE	.24	.34							
CV	2.01	3.14							
n	22	25							
Length of digit four									
Mean	46.05	44.04			Sex	1	47.064	4.00	.052
SD	3.36	3.49			Within	45	11.776		
SE	.72	.70							
CV	7.30	7.92							
n	22	25							
Length of digit five									
Mean	33.64	32.96			Sex	1	5.353	1.91	.968
SD	1.59	1.74			Within	45	2.801		
SE	.34	.35							
CV	4.73	5.28							
n	22	25							
Tibia length									
Mean	10.27	10.04			Sex	1	.634	1.34	.254
SD	.63	.74			Within	45	.474		
SE	.14	.15							
CV	6.13	7.37							
n	22	25							
Calcar length									
Mean	9.09	8.60			Sex	1	2.820	2.77	.103
SD	1.15	.87			Within	45	1.018		
SE	.25	.17							
CV	12.65	10.12							
n	22	25							

Table 28.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Greatest length of skull									
Mean	14.11	13.47			Sex	1	4.485	38.05	<.001
SD	.35	.34			Within	41	.118		
SE	.08	.07							
CV	2.48	2.52							
n	21	22							
Condylobasal length									
Mean	13.91	13.25			Sex	1	4.738	49.40	<.001
SD	.31	.31			Within	41	.096		
SE	.07	.07							
CV	2.23	2.34							
n	21	22							
Zygomatic breadth									
Mean	9.76	9.31			Sex	1	1.290	20.31	<.001
SD	.25	.25			Within	24	.064		
SE	.07	.08							
CV	2.56	2.69							
n	15	11							
Postorbital constriction									
Mean	3.36	3.29			Sex	1	.059	7.01	.011
SD	.10	.08			Within	45	.008		
SE	.02	.02							
CV	2.98	2.43							
n	22	25							
Mastoid breadth									
Mean	9.60	9.06			Sex	1	2.143	19.92	<.001
SD	.40	.22			Within	28	.108		
SE	.10	.06							
CV	4.17	2.43							
n	16	14							
Breadth of braincase									
Mean	7.08	6.81			Sex	1	.768	14.58	<.001
SD	.28	.18			Within	41	.053		
SE	.06	.04							
CV	3.95	2.64							
n	21	22							
Rostral breadth									
Mean	4.33	3.88			Sex	1	2.431	49.88	<.001
SD	.22	.22			Within	45	.049		
SE	.05	.04							
CV	5.08	5.67							
n	22	25							
Height of braincase									
Mean	6.08	5.94			Sex	1	.203	3.19	.082
SD	.27	.24			Within	44	.064		
SE	.06	.05							
CV	4.44	4.04							
n	20	22							
Breadth across the upper molars									
Mean	6.54	6.40			Sex	1	.246	12.29	.001
SD	.13	.15			Within	44	.020		
SE	.03	.03							
CV	1.99	2.34							
n	21	25							

Table 28.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Breadth across the upper canines									
Mean	3.92	3.56			Sex	1	1.457	65.91	<.001
SD	.15	.15			Within	43	.022		
SE	.03	.03							
CV	3.83	4.21							
n	21	24							
Length of the maxillary toothrow									
Mean	5.57	5.34			Sex	1	.607	28.30	<.001
SD	.16	.13			Within	44	.022		
SE	.04	.03							
CV	2.87	2.43							
n	21	25							
Length of the upper molariform toothrow									
Mean	4.27	4.20			Sex	1	.058	2.84	.099
SD	.12	.16			Within	44	.021		
SE	.03	.03							
CV	2.81	3.81							
n	21	25							
Width of the widest molar									
Mean	2.00	1.96			Sex	1	.014	2.31	.135
SD	.08	.08			Within	44	.006		
SE	.02	.02							
CV	4.00	4.08							
n	21	25							
Greatest length of the mandible									
Mean	10.56	10.25			Sex	1	1.020	10.28	.003
SD	.33	.30			Within	42	.099		
SE	.07	.06							
CV	3.13	2.93							
n	22	22							
Length of the maxillary toothrow									
Mean	5.91	5.69			Sex	1	.965	69.28	<.001
SD	.10	.13			Within	43	.014		
SE	.02	.03							
CV	1.69	2.28							
n	21	24							
Length of the coronoid process									
Mean	3.76	3.46			Sex	1	.950	25.87	<.001
SD	.22	.15			Within	41	.037		
SE	.05	.03							
CV	5.85	4.34							
n	22	21							

acters and statistically significant differences were detected for all but three of these characters. *N. mattogrossensis* is clearly dimorphic with males being larger than females.

Molossus ater (E. Geoffroy, 1805)

This molossid aerial insectivore was rare in the Caatingas and was apparently absent from the Chapada do Araripe. Only one specimen, a juvenile, was captured from the Caatingas in December.

Molossus molossus (Pallas, 1766)

This fast-flying aerial insectivore was common in both Caatingas and Cerrado biomes. In both regions of the Northeast, *M. molossus* reached highest densities near abandoned man-made structures that it utilized for roosts. The sex ratios within Caatingas and Cerrado biomes were equal (Binomial Test, $P > .05$). Approximately 51% of the 135 captured adult specimens from the Chapada do Araripe were males; similarly, 50% of the 64 captured adult specimens from the Caatingas were males.

Samples are sufficiently large to permit a statistical analysis of individual, secondary sexual, and geographic variation in specimens of *M. molossus* from the Northeast of Brazil; the results are summarized in Table 29. Males have larger sample means than females for 26 of the 29 variables; six external and 16 cranial characters exhibit statistically significant secondary sexual variation. Like other molossids, *M. molossus* is highly dimorphic with males larger than females. Approximately half of the characters analyzed have larger sample means in the Caatingas than in the Cerrado, nine of that group exhibit statistically significant geographic variation. Only three characters have larger sample means in the Cerrado than in the Caatingas and only one of those variables exhibits statistically significant geographic variation. Geographic dimorphism is pronounced in the Northeast with Caatingas populations being larger on the average than Cerrado populations.

Eumops sp.

This molossid aerial insectivore was rare in the Caatingas and absent from the Chapada do Araripe. The single specimen from the Caatingas was taken in December; because of a damaged skull, specific status could not be ascertained with confidence.

MORPHOMETRICS

Throughout this study, morphometric variation has been analyzed using statistical techniques. Indeed, the consistent application of statistical criteria distinguishes this work from most other studies. Two interrelated questions naturally arise concerning such an approach: 1) does statistical significance mean biological significance? and 2) does biological significance mean statistical significance? The answer to both questions lies in exactly understanding the way in which biologists ask questions about the natural world.

Frequently, one is interested in various biological characteristics of a large population (for example, a species, subspecies, population, sex, or age group), but due to various limitations, only a small portion of the entire population can feasibly be examined. As such, samples are utilized to infer information about the populations from which they were derived. Further, samples are used in order to compare characteristics of two or more populations. Whenever samples are utilized to infer knowledge about larger populations, random error in selecting a sample affects the observed sample characteristics. The application of statistical techniques allows the biologist to ascertain with a prescribed level of confidence whether observed differences between samples could be due to chance or due to true differences in the populations from which they were derived. Clearly, perceived differences between samples which are caused by chance ought not to denote biological differences between the populations from which the samples were taken; the observed differences between the samples are due to chance. When statistical differences cannot be shown for a particular analysis, then the data do not support the existence of any population differences. The failure of a statistical test to detect a real difference between the populations is related to Type II error or β error (Sokal and Rohlf, 1969). Small samples make it difficult to detect real differences between populations; hence, very small differences between populations require large samples in order to be detected. Incorrectly ascribing differences to a population based upon sample characteristics is related to Type I error or α error (Sokal and Rohlf, 1969). Even when statistical significance is obtained, there is a known chance of being incorrect (that is, the populations may not be different at all). The exact chance of incorrectly asserting a difference between populations which does not, in fact, exist is equal to the level of significance of the statistical test (for example the 'P' level). Statistical differences detected with small samples are as valid as statistical differences detected with large samples because the probability of the differences being due to chance is defined by the Type I error.

In summary, statistical analysis is a method of considering the effects of chance in an investigation utilizing samples. Statistical significance indicates that the observed sample differences are *not* due to chance, while a failure to obtain statistical significance infers that any observed differences between samples are indistinguishable from chance variations. The biological meaning of the results is predicated upon a choice of characters with biological significance. If the character has biological meaning, then a significant statistical test reveals true differ-

Table 29.—*Summary statistics for external and cranial characters (mean; standard deviation, SD; standard error of the mean, SE; coefficient of variation, CV; sample size, n) of* Molossus molossus *males and females from both Caatinga and Cerrado biomes. A two-way analysis of variance (Model I) with replication is presented for each character. The existence of significant secondary sexual or geographic variation is indicated by* P *values less than or equal to .050.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Total length									
Mean	108.20	102.90	106.30	101.75	Area	1	46.513	3.79	.055
SD	3.41	3.41	4.00	3.13	Sex	1	485.113	39.52	<.001
SE	.76	.76	.90	.70	A × S	1	2.813	.23	.634
CV	3.15	3.31	3.76	3.08	Error	76	12.276		
n	20	20	20	20					
Tail length									
Mean	37.60	33.95	38.10	35.70	Area	1	25.313	2.11	.151
SD	2.60	2.82	3.48	4.61	Sex	1	183.013	15.22	<.001
SE	.58	.63	.78	1.03	A × S	1	7.813	.65	.423
CV	6.91	8.31	9.13	12.91	Error	76	12.023		
n	20	20	20	20					
Hindfoot length									
Mean	7.45	6.75	6.95	7.00	Area	1	.313	.57	.453
SD	.69	.91	.83	.46	Sex	1	2.113	3.85	.053
SE	.15	.20	.19	.10	A × S	1	2.813	5.13	.026
CV	9.26	13.48	11.94	6.57	Error	76	.548		
n	20	20	20	20					
Ear length									
Mean	13.75	13.25	13.55	13.10	Area	1	.613	1.65	.203
SD	.55	.72	.61	.55	Sex	1	4.513	12.14	<.001
SE	.12	.16	.14	.12	A × S	1	.012	.03	.855
CV	4.00	5.43	4.50	4.20	Error	76	.372		
n	20	20	20	20					
Tragus length									
Mean	1.95	2.00	1.95	1.90	Area	1	.050	.67	.417
SD	.22	0	.22	.45	Sex	1	.000	.00	.999
SE	.05	0	.05	.10	A × S	1	.050	.67	.417
CV	11.28	0	11.28	23.68	Error	76	.075		
n	20	20	20	20					
Forearm length									
Mean	40.95	39.95	40.60	40.20	Area	1	.050	.04	.836
SD	.83	1.43	1.00	.95	Sex	1	9.800	8.47	.005
SE	.19	.32	.22	.21	A × S	1	1.800	1.56	.216
CV	2.03	3.58	2.46	2.36	Error	76	1.156		
n	20	20	20	20					
Weight									
Mean	16.67	15.15	15.98	13.33	Area	1	31.878	10.65	.002
SD	1.29	1.95	1.77	1.84	Sex	1	87.153	29.11	<.001
SE	.29	.44	.40	.41	A × S	1	6.328	2.11	.150
CV	7.74	12.87	11.07	13.80	Error	76	2.994		
n	20	20	20	20					
Length of digit one									
Mean	6.55	6.15	6.85	6.70	Area	1	3.613	9.08	.003
SD	.60	.49	.81	.57	Sex	1	1.513	3.80	.055
SE	.13	.11	.18	.13	A × S	1	.313	.79	.378
CV	9.16	7.97	11.82	8.51	Error	76	.398		
n	20	20	20	20					

Table 29.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Length of digit three									
Mean	77.85	76.35	76.00	75.40	Area	1	39.200	5.30	.024
SD	2.03	2.39	2.49	3.68	Sex	1	22.050	2.98	.088
SE	.46	.53	.56	.83	A × S	1	4.050	.55	.462
CV	2.61	3.13	3.28	4.88	Error	76	7.393		
n	20	20	20	20					
Length of digit four									
Mean	58.15	57.60	57.05	56.50	Area	1	24.200	3.92	.050
SD	1.84	2.62	2.46	2.89	Sex	1	6.050	.98	.330
SE	.41	.59	.55	.65	A × S	1	.000	.00	1.000
CV	3.16	4.55	4.31	5.12	Error	76	6.175		
n	20	20	20	20					
Length of digit five									
Mean	41.85	41.40	40.80	40.65	Area	1	16.200	5.67	.020
SD	1.66	2.09	1.47	1.46	Sex	1	1.800	.63	.430
SE	.37	.47	.33	.33	A × S	1	.450	.16	.693
CV	3.97	5.04	3.60	3.59	Error	76	2.857		
n	20	20	20	20					
Tibia length									
Mean	15.20	14.55	15.30	14.85	Area	1	.800	2.44	.122
SD	.52	.69	.57	.49	Sex	1	6.050	18.47	<.001
SE	.12	.15	.13	.11	A × S	1	.200	.61	.437
CV	3.42	4.74	3.73	3.30	Error	76	.328		
n	20	20	20	20					
Calcar length									
Mean	14.10	12.95	13.15	13.35	Area	1	1.513	.70	.405
SD	2.02	1.28	1.23	1.18	Sex	1	4.513	2.09	.152
SE	.45	.29	.27	.26	A × S	1	9.113	4.23	.043
CV	14.33	9.88	9.35	8.84	Error	76	2.160		
n	20	20	20	20					
Greatest length of skull									
Mean	16.92	16.24	16.95	15.97	Area	1	.276	1.77	.187
SD	.36	.39	.45	.37	Sex	1	13.695	87.89	<.001
SE	.08	.09	.10	.08	A × S	1	.435	2.79	.099
CV	2.13	2.40	2.65	2.32	Error	76	.156		
n	20	20	20	20					
Condylobasal length									
Mean	15.63	14.80	15.49	14.53	Area	1	.903	8.81	.004
SD	.35	.30	.35	.28	Sex	1	15.931	155.34	<.001
SE	.08	.07	.08	.06	A × S	1	.091	.89	.349
CV	2.24	2.03	2.26	1.93	Error	76	.103		
n	20	20	20	20					
Zygomatic breadth									
Mean	11.00	10.53	10.86	10.35	Area	1	.496	10.26	.002
SD	.25	.20	.25	.18	Sex	1	4.851	100.31	<.001
SE	.05	.04	.05	.04	A × S	1	.006	.13	.723
CV	2.27	1.90	2.30	1.74	Error	76	.048		
n	20	20	20	20					
Postorbital constriction									
Mean	3.56	3.52	3.62	3.48	Area	1	.001	.04	.833
SD	.18	.14	.17	.15	Sex	1	.171	6.81	.011
SE	.04	.03	.04	.03	A × S	1	.055	2.19	.143
CV	5.06	3.98	4.70	4.31	Error	76	.025		
n	20	20	20	20					

Table 29.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
Mastoid breadth									
Mean	10.58	10.19	10.53	10.06	Area	1	.153	2.37	.128
SD	.22	.20	.31	.28	Sex	1	3.741	57.85	<.001
SE	.05	.05	.07	.06	A × S	1	.036	.56	.457
CV	2.08	1.96	2.94	2.78	Error	76	.065		
n	20	20	20	20					
Breadth of braincase									
Mean	8.84	8.63	8.96	8.56	Area	1	.013	.32	.573
SD	.16	.16	.27	.18	Sex	1	1.861	47.69	<.001
SE	.04	.04	.06	.04	A × S	1	.200	5.13	.026
CV	1.81	1.85	3.01	2.10	Error	76	.039		
n	20	20	20	20					
Rostral breadth									
Mean	5.17	5.09	5.28	4.99	Area	1	.001	.03	.870
SD	.17	.18	.21	.23	Sex	1	.66	16.84	<.001
SE	.04	.04	.05	.05	A × S	1	.210	5.31	.020
CV	3.29	3.54	3.98	4.61	Error	76			
n	20	20	20	20					
Height of braincase									
Mean	9.77	9.24	9.63	9.03	Area	1	.578	8.72	.004
SD	.19	.25	.32	.25	Sex	1	.385	96.37	<.001
SE	.04	.06	.07	.06	A × S	1	.025	.37	.545
CV	1.94	2.71	3.32	2.77	Error	76	.066		
n	20	20	20	20					
Breadth across the upper molars									
Mean	7.96	7.68	7.86	7.59	Area	1	.171	4.16	.045
SD	.16	.14	.29	.19	Sex	1	1.485	36.09	<.001
SE	.04	.03	.06	.04	A × S	1	.000	.00	.956
CV	2.01	1.82	3.69	2.50	Error	76	.041		
n	20	20	20	20					
Breadth across the upper canines									
Mean	4.48	4.34	4.50	4.20	Area	1	.066	2.37	.128
SD	.14	.17	.20	.15	Sex	1	1.035	37.10	<.001
SE	.03	.04	.05	.03	A × S	1	.120	4.31	.041
CV	3.13	3.92	4.44	3.57	Error	76	.027		
n	20	20	20	20					
Length of the maxillary toothrow									
Mean	6.22	5.97	6.25	5.96	Area	1	.001	.02	.896
SD	.11	.22	.20	.13	Sex	1	1.458	50.53	<.001
SE	.03	.05	.05	.03	A × S	1	.008	.28	.600
CV	1.77	3.69	3.20	2.18	Error	76	.029		
n	20	20	20	20					
Length of the upper molariform toothrow									
Mean	4.87	4.78	4.93	4.74	Area	1	.003	.16	.689
SD	.12	.12	.19	.11	Sex	1	.378	19.58	<.001
SE	.03	.03	.04	.02	A × S	1	.055	2.85	.095
CV	2.46	2.51	3.85	2.32	Error	76	.019		
n	20	20	20	20					
Width of the widest molar									
Mean	2.19	2.15	2.16	2.11	Area	1	.025	3.03	.086
SD	.11	.08	.07	.10	Sex	1	.041	5.01	.208
SE	.02	.02	.02	.02	A × S	1	.001	.06	.804
CV	5.02	3.72	3.24	4.74	Error	76	.008		
n	20	20	20	20					

Table 29.—*Continued.*

	Caatinga		Cerrado		Analysis of variance				
	♂♂	♀♀	♂♂	♀♀	Factor	df	MS	F	Significance
					Greatest length of the mandible				
Mean	12.04	11.51	12.02	11.19	Area	1	.613	10.10	.002
SD	.26	.23	.23	.26	Sex	1	9.248	152.43	<.001
SE	.06	.05	.05	.06	A × S	1	.481	7.92	.006
CV	2.16	2.00	1.91	2.32	Error	76	.061		
n	20	20	20	20					
					Length of the mandibular toothrow				
Mean	6.97	6.61	6.85	6.52	Area	1	.231	8.02	.006
SD	.14	.20	.18	.15	Sex	1	2.346	81.44	<.001
SE	.03	.05	.04	.03	A × S	1	.003	.11	.743
CV	2.01	3.03	2.63	2.30	Error	76	.029		
n	20	20	20	20					
					Length of the coronoid process				
Mean	4.57	4.34	4.50	4.29	Area	1	.066	1.61	.208
SD	.14	.13	.23	.28	Sex	1	.946	23.06	<.001
SE	.03	.03	.05	.06	A × S	1	.003	.08	.783
CV	3.06	2.93	5.11	6.53	Error	76	.041		
n	20	20	20	20					

ences in a biologically important characteristic. Failure to detect a statistically significant difference between samples infers that no real difference exists, or that if it does exist, the magnitude of the difference is too small to be detected by samples of the size utilized in the investigation.

Microgeographic Variation

Phenotypic variation within populations is the raw material upon which Natural Selection operates. However, only that portion of the phenotypic variation under genetic control is affected by Natural Selection. Unfortunately, a strong correlation between genic variation (estimated by electromorph heterozygosity) and morphological variation in mammalian populations has not been convincingly demonstrated (for a critical review, see Schnell and Selander, 1981); rather, it appears that genic, karyotypic and morphological evolution progress independently of each other. In part, the disparity between genic and morphological variation may be ascribed to regulator genes which greatly affect morphology but are not sampled by electrophoretic studies. Nonetheless, only by comparing variation in different populations can one determine how and to what extent the differences between individuals are molded into the differences that separate races and species (Simpson, 1944; Mayr, 1964; Yablokov, 1974). The consensus appears to be that the fields of population and quantitative genetics have not progressed in a direction to aid in the interpretation of these dynamics (Sokal, 1977). Two approaches to the problem have been suggested (Falconer, 1972)—first, new techniques in quantitative biology need to be developed in order to analyze patterns of natural variation; and second, a wider variety of characters and organisms need to be examined in order to decide which phenomena are general and which may be attributed to special circumstances. This study reveals the extent and magnitude of variation present within and between chiropteran populations in close geographic proximity. As such, it aids in illuminating general patterns of meristic variation present in natural populations, which both Mayr (1964) and Falconer (1972) suggested as a prerequisite for understanding evolutionary dynamics.

Nine bat species from the Brazilian Northeast were caught in sufficient quantities to permit statistical analyses of mean differences between populations from Caatingas and Cerrado biomes. The α level (Type I error) specified for each statistical test predetermines the probability of detecting differences between populations which occur because of chance alone. When 30 different morphometric characters are being statistically analyzed for mean differences, an average of 1.5 (.05 by 30) of the tests should incorrectly indicate that the means are different (if the tests are independent), when in fact they are not. Although some of the tests for some of the species may not be independent, this relation was utilized to determine the minimum number of statistical differences required to indicate the presence of real differences between Caatingas and Cerrado populations. If the assumption of independence is correct, the occurrence of 5 or more characters with statistically different means should occur less than one percent of the time due to chance alone. As a conservative measure then, only bat species with 5 or more significant differences were indicated as exhibiting geographic size dimorphism because pronounced correlation among the characters would increase the probability of mistakenly detecting significance. Five bat species did exhibit geographic size dimorphism for at least five morphometric characters. Caatingas populations were larger than Cerrado populations in four species—*C. perspicillata* (Table 16), *V. lineatus* (Table 18), *A. jamaicensis* (Table 20), and *M. molossus* (Table 29)—whereas *A. geoffroyi* (Table 15) exhibited geographic size dimorphism in which the Cerrado population was larger than the Caatingas population. These results caution against pooling data from different localities whenever possible in order to detect age- or sex-related differences. Further, they indicate that appreciable morphometric divergence can exist between populations of highly mobile species even when these populations inhabit adjacent areas. This implies that the amount of genetic communication between populations of these five species is quite low; Ehrlich and Raven (1969) considered this phenomenon to have impact upon the very definition of a biological species.

The utilization of statistical analysis can be a powerful tool in systematics, however, it should not form the sole basis upon which decisions concerning subspecific status are evaluated. Most populations will have at least slightly different parametric mean values because of the combined effects of mutation, migration, drift and natural selection acting upon local populations. The ability to detect these differences, even if they are slight, increases with sample size and the sensitivity of the utilized statistical procedure. Hence, the elucidation of statistical differences between populations often only confirms the original supposition that the samples were drawn from biological populations with different mean values. Clearly, the decision to apply subspecific designation to taxa must go beyond the detection of statistical differences because different populations within a subspecies could also exhibit such differences.

Secondary Sexual Variation

Although biologists have been interested in sexual dimorphism for many years, distinctions between the causes and functions of the phenomenon frequently are not evident. Polygamous mating systems, differential rates of maturation, unequal sex ratios, and differential resource utilization are often associated with species exhibiting dimorphism (Sealander, 1957; Daly and Wilson, 1978). A number of hypotheses which are not mutually exclusive have been developed to account for dimorphism in naturally occurring populations. The most prominent hypothesis, originally promulgated by Darwin (1859, 1871*a*, 1871*b*), suggests that one sex usually competes for reproductive access to the opposite sex. This results in different selective regimes acting on the competitors and on the objects of competition (see Trivers, 1972; Wilson, 1975; and Ralls, 1976 for reviews). Trivers (1972) hypothesized that the sex with the greatest parental investment will be in short supply and thereby be the object of competition. Due to their limited parental investment, male mammals should compete among themselves for the available females. Because large size often is beneficial in agonistic encounters, selection should differentially favor a larger size in males than in females. An alternative hypothesis suggests that sexual dimorphism reduces intraspecific competition for resources (Selander, 1966, 1972). Examples in the literature for skates (Feduccia and Slaughter, 1974), fish (Keast, 1966), lizards (Schoener, 1967, 1968), birds (Rand, 1952; Selander, 1966, 1972; Earhart and Johnson, 1970) and mammals (Kummer, 1971) have linked body size differences between males and females to differences in food consumption. In contrast, Mares and Williams (1977) found that different sized individuals within various granivorous rodent species did not consume different sized seeds. Moreover, Husar (1976) described dietary differences between male and female vespertilionid bats in which the differences in diet were in prey type rather than in prey size. Williams and Findley (1979) have shown that males and females in the species examined by Husar (1976) were not dimorphic. Thus, even if the sexes do differentially utilize resources, partitioning need not occur by prey size and sexual size dimorphism need not be the mechanism promoting the differences in diet.

If size variation can reduce intraspecific competition, it is not clear why greater individual variation, without sex associated differences, could not accomplish the same results. All other circumstances being equal, there is no *a priori* reason to expect males to be larger than females or females to be larger than males as a result of the differential niche hypothesis. At best, once other factors initially select for sex-related size differences, these differences could be accentuated by the benefits of reduced resource competition by niche partitioning among the sexes.

The observation that females are frequently larger than males has revealed the general inadequacy of both the sexual selection and niche partitioning hypotheses. Ralls (1976) advances the "Big Mother" hypothesis to account for cases of sexual size dimorphism in which females are larger than males. For a variety of reasons, a larger female may be a more fit mother (that is, produce a larger number of successful progeny). Larger mothers may produce offspring with greater weights at birth; provide more or higher quality milk; more efficiently transport or defend young; or maintain homeothermic equilibrium conducive to embryonic development. Myers (1978) examined size variation in vespertilionid bats and only found dimorphism in which females were significantly larger than males. His analyses further showed that the wings of females were proportionately larger than those of males, with the degree of dimorphism correlated with litter size. Because of these observations, Myers (1978) suggested that the demands of motherhood were greater on species producing multiple young. Williams and Findley (1979) contend that the data considered by Myers (1978) were biased because monomorphic species with multiple young and highly dimorphic species with single young were excluded from the analyses. In their work (Williams and Findley, 1979), correlations between litter size and the degree of dimorphism were not evident. In accord with the work of Bogan (1975) and Findley and Traut (1970), they conclude that dimorphism in vespertilionids is probably related to differential thermoregulation rather than wing loading.

Within the Chiroptera, sexual dimorphism is primarily restricted to size, although the possession of dimorphic glands in the Emballonuridae and Molossidae is quite common (Bradbury, 1977). Sixteen species of bats from the Northeast of Brazil exhibited significant secondary sexual variation for eight or more morphometric characters. In approximately one-third of those cases, the sample means of females were larger than the sample means of the males (*P. macrotis,* Table 3; *G. soricina,* Table 13; *L. mordax,* Table 14; *V. lineatus,* Table 18; *A. concolor,* Table 19; *D. rotundus,* Table 22; *L. borealis,* Table 25). Male sample means were larger than those of females for the other species in which statistically significant dimorphism was detected (*N. leporinus,* Table 4; *T. silvicola,* Table 8; *P. discolor,* Table 10; *P. hastatus,* Table 11; *A. geoffroyi,* Table 15; *S. lilium,* Table 17; *A. jamaicensis,* Table 20; *N. mattogrossensis,* Table 28; *M. molossus,* Table 29). Clearly, dimorphism for size is common among the Chiroptera, and unlike the situation in many vertebrate orders, females are frequently significantly larger than males. Ralls (1976) summarizes our knowledge of sexual dimorphism in bats in which the females have been implicated to be larger than males while Myers (1978) and Williams and Findley (1979) present additional information on bats in the family Vespertilionidae. Statistically significant dimorphism has only been substantiated for 12 of the 45 potential cases that Ralls reports. Three of the species implicated as having larger females than males either show little size dimorphism (*A. lituratus*) or exhibit statistically significantly dimorphism in which the males are actually larger than the females (*A. geoffroyi* and *A. jamaicensis*) in populations from Brazil. The data for *D. rotundus* and *L. borealis* substantiates Ralls' (1976) claim that females are larger than males in these species. Further, this study adds five different species to Ralls' list of bats in which females are larger than males (*P. macrotis, G. soricina, L. mordax, V. lineatus, A. concolor*).

Most authors agree that both selection pressures consistent with the hypothesis of sexual selection and the "Big Mother" hypothesis affect to greater or lesser extents the observed size relations between the sexes. The data from this study indicates that selective pressures favoring large females are more common than generally perceived for the Chiroptera. Knowledge of bat behaviour and natural history is somewhat limited, but it does *not* suggest a reversal of the theoretical conditions in which males compete among themselves for females (see Bradbury, 1977). Indeed, male bats invest very little in their offspring other than the time and energy involved in copulation (see Kleiman and Malcolm, 1981). In those cases where behaviour patterns have been elucidated, it appears that males compete among themselves for access to reproductive females (Bradbury, 1977). By implication, sexual selection is probably not the dominant factor producing larger females. However, it may well be the factor that reduces the observed differences between the sexes in those cases where females are statistically larger than males. Although Myers (1978) and Williams and Findley (1979) disagree in detail about the particular factors that affect dimorphism in vespertilionids, both attribute the observed differences to biological conditions consistent with the "Big Mother" hypothesis. This study cannot distinguish between the thermoregulatory hypothesis favored by Williams and Findley (1979) and the wing-loading hypothesis of Myers (1978); however, it can qualify some of the contentions they presented. Myers (1978) conjectures that small molossids should show reduced sexual dimorphism (males larger than females) compared to larger species in the family because they share certain flight and feeding characteristics with the Vespertilionidae. In the two species of molossids with sufficiently large samples to permit statistical analyses (*M. molossus* and *N. mattogrossensis*), the males are consistently larger and statistically different than females for both cranial and external characters. Further, *N. mattogrossensis* is one of the smallest members of the Molossidae and it clearly does not exhibit the reduced dimorphism predicted by Myers (1978). Similarly, Williams and Findley (1979) reject Myers' contention by showing that lasiurine bats in the family Verspertilionidae do not exhibit reduced dimorphism (females larger than males) although they would be predicted to do so by Myers' reasoning. The morphometric analyses of *P. macrotis* from the Caatingas are in accord with the observations of Myers (1978) and others (see Bradbury, 1977) for Emballonurids; this small bat is dimorphic with females larger than males. Of course, the proponents of the thermoregulatory hypothesis could also claim that the data supports their position since the demands of thermoregulation are accentuated for small species. Obviously, more data need to be collected from vespertilionid populations occurring along latitudinal or altitudinal gradients to see if species with eurythermal distributions exhibit degrees of dimorphism which are enhanced as temperature decreases.

Although not nearly as pervasive as in the Vespertilionidae, the incidence of sexual dimorphism with females larger than males is also common in the Phyllostomidae (in contrast, see the comments of Bradbury, 1977). Females are larger than males in five of the eleven species exhibiting statistically significant secondary sexual dimorphism. Within the various phyllostomid subfamilies, it appears that smaller species tend to be dimorphic with females larger than males, whereas larger species tend to exhibit dimorphism with larger males. Although Myers (1978) suggests a relation between feeding ecology and dimorphism, little evidence is available to support that position within the Phyllostomidae. The occurrence of dimorphism within a subfamily does not seem to be related to the feeding strategies of the constituent species.

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WILLIAM W. KORTH

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ABSTRACT

All known North American rodents from the late Paleocene and early Eocene are reviewed. Four families are recognized, Ischyromyidae, Sciuravidae, ?Eutypomyidae, and ?Cylindrodontidae. This is the first recognition of the latter two families in the early Eocene. The previously proposed infraorder of rodents, the Franimorpha, is here believed to be composed of members of the Sciuromorpha, and thus does not exist as a distinct taxon.

Five new genera are described, four ischyromyids (*Notoparamys, Quadratomus, Acritoparamys, Apatosciuravus*) and one ?eutypomyid (*Mattimys*), along with eight new species, *Paramys simpsoni, Thisbemys elachistos, Notoparamys arctios, Reithroparamys ctenodactylops, Microparamys reginensis, M. scopaiodon, Apatosciuravus bifax,* and *Franimys ambos.*

Rodents are believed to have originated from an Asian ctenodactyloid-like ancestor rather than a paramyine ancestor, as previously believed. Reithroparamyinae are believed to represent the most primitive ischyromyids, from which the Ischyromyinae and all other subfamilies of the Ischyromyidae can be derived. Ischyromyids do not represent the basal stock from which all later rodents were derived, but may be involved in the ancestry of some later groups of rodents such as the sciurids, eutypomyids, castorids, and the European glirids.

INTRODUCTION

Cope (1877, 1884) was the first to recognize rodents from the early Eocene of North America. He identified three species and referred them to the European genus *Plesiarctomys* Bravard (1850). Two of these species had been described earlier by Leidy (1871) from the middle Eocene, *P. delicatus* and *P. delicatissimus,* and one was new, *P. buccatus.* Loomis (1907) recognized seven new species of *Paramys* Leidy (1871) and one species of *Sciuravus* Marsh (1872) from the "Wasatch" and Wind River Formations of Wyoming. He only questionably accepted Cope's (1877) species *Plesiarctomys*? *buccatus* from the early Eocene of New Mexico.

The only systematic review of early Eocene rodents since Cope's (1884) treatment of all Tertiary mammals of the western United States was by Matthew (1918) as a part of his overall revision with Granger of early Eocene mammals of North America. Matthew (1918) synonymized many of Loomis' species of *Paramys* and introduced two new species, one of *Paramys, P. murinus,* and one of *Mysops* Leidy (1871), *M. kalicola.* Matthew failed, however, to discuss Loomis' (1907) species of *Sciuravus, S. depressus.*

Matthew (1910) and Wilson (1949) discussed early Eocene rodents in their discussions of the early evolution of rodents but offered no major systematic changes. The majority of the new species and systematic reviews of early Eocene rodents have been included in systematic studies of entire faunas (Kelley and Wood, 1954; Gazin, 1952, 1962; Guthrie, 1967, 1971; Rose, 1981) or rodents from a particular fauna (Jepsen, 1937; Gazin, 1961; Wood, 1965). Wood (1962) presented a major review of the "Paramyidae," in which he recognized eight genera and 23 species or subspecies from the early Eocene and latest Paleocene. He did not discuss the early Eocene Sciuravidae or *Mysops kalicola* Matthew (1918) in his review.

All species discussed in this study are from the early Eocene with one species from the latest Paleocene. Granger (1910, 1914) proposed several faunal levels in the early Eocene of North America—Clarkfork, Sand Coulee, Graybull, Lysite, and Lost Cabin (from oldest to youngest). H. E. Wood et al. (1941) proposed the provincial term Wasatchian for the North American early Eocene, and referred Granger's Clarkfork to the latest Paleocene. Van Houten (1945) presented a thorough comparison of the faunas from the Clarkforkian and the Wasatchian. He recognized only three of Granger's faunal levels, Graybull, Lysite, and Lost Cabin, within the Wasatchian and maintained the Clarkforkian as latest Paleocene.

Robinson (1966), in his faunal study of the Huerfano Formation of Colorado, proposed the term Gardnerbuttean for a fourth and uppermost faunal level of the Wasatchian. The Gardnerbuttean was based on the mammalian fauna from the Upper Huerfano Formation.

In a series of papers by workers from the University of Michigan (summarized most recently by Rose, 1981), the Clarkforkian was proposed as representing the earliest Eocene.

The faunal divisions of the early Eocene accepted here are—Graybullian, Lysitean, Lostcabinian, and Gardnerbuttean, as substages of the Wasatchian. The Clarkforkian is accepted here only provisionally as representing the early Eocene, and may be equivalent to the early Graybullian of Van Houten (1945).

Because rodents have been used, at least in part, in separating different faunal levels of the early Eocene and latest Paleocene (Van Houten, 1945; Robinson, 1966; Guthrie, 1971; Rose, 1981) and no overall systematic review of these rodents has been presented for over 60 years (Matthew, 1918), a reexamination of the systematics of this group of mammals is necessary.

Tooth nomenclature used in discussion is after Wood and Wilson (1936). All dental measurements are in millimeters.

Abbreviations used: ACM—Pratt Museum, Amherst College; AMNH—American Museum of Natural History; CM—Carnegie Museum of Natural History; CU—University of Colorado Museum of Geology; FMNH—Field Museum of Natural History; KU—University of Kansas Natural History Museum; MCZ—Museum of Comparative Zoology, Harvard University; PU—Princton University; ROM—Royal Ontario Museum; TMM—Texas Memorial Museum; TTM—Museum of Texas Tech University; UCMP—University of California Museum of Paleontology; UMMP—University of Michigan Museum of Paleontology; USNM—U.S. National Museum of Natural History; UW—University of Wyoming Museum of Geology; WAM—Webb School, Alf Museum; YPM—Yale Peabody Museum; N—number of specimens; M—mean; S—standard deviation; V—coefficient of variation; OR—observed range; a-p—anteroposterior length; tra—anterior transverse width; trp—posterior transverse width.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Suborder Sciuromorpha Brandt, 1855

Discussion.—In his 1955 classification, Wood included the primitive ischyromyoid rodents (paramyids, ischyromyids, cylindrodontids, sciuravids, protoptychids, and phiomyids) in the suborder Sciuromorpha, one of Brandt's (1855) original three suborders which also included the sciurids and aplodontids. Later, Wood (1937, 1958, 1962) included the ischyromyoids in the Protrogomorpha of Zittel (1893) along with the aplodontoids. In a classification of the Ischyromyidae (including Wood's Paramyidae), Black (1971) included the family in the Sciuromorpha without discussion. Sciuromorpha is used here in the same sense as it was by Wood (1955) with the exclusion of Phiomyidae.

Wood (1975) revised his classification of rodents and accepted the two-fold subordinal division of the rodents proposed by Tullberg (1899)—Hystricognathi and Sciurognathi. He (Wood, 1975) erected a new infraorder Franimorpha based predominantly on the presence of an "incipiently" hystricognathous mandible, and included the Reithroparamyinae (*sensu* Wood, 1962), *Prolapsus* Wood (1973), *Protoptychus* Scott (1895), and *Guanajuatomys* Black and Stephens (1973) in the Franimorpha. Later, the Cylindrodontidae were also included in the Franimorpha (Wood, 1980, 1981).

Wood (1975) included the Paramyidae (excluding the Reithroparamyinae) in the infraorder Protrogomorpha of the suborder Sciurognathi, while maintaining the Reithroparamyinae as a subfamily of the Paramyidae. Finally, he (Wood, 1981) raised the Reithroparamyinae to the family level to avoid the ambiguity of having a single family in two different suborders.

None of the species included in the Franimorpha (Wood, 1975, 1980) appear to have attained hystricognathy as defined by Tullberg (1899). The holotype of *Franimys amherstensis,* the species on which the infraorder is based, includes the posterior half of a right mandible without teeth (ACM 10524). This specimen, however, is badly broken and calcite has filled and expanded many of the cracks distorting the shape of the mandible (Fig. 20), thus making it impossible to determine the original position of the angle. The only referred mandible of *F. amherstensis* (ROM 2180) identified by Wood (1962) is sciurognathous. This specimen, however, is not *F. amherstensis* and is referred below to *Acritoparamys atwateri* (Loomis, 1907).

Dawson (1977) noted that the mandible of *Reithroparamys,* considered hystricognathous by Wood (1962), was fully sciurognathous and not "incipiently" hystricognathous. In other members of Wood's (1962) Reithroparamyinae, the incipient or subhystricognathy is truly sciurognathy. The angle of the mandible is not positioned lateral to the horizontal ramus as in true hystricognathous rodents. The mandible of these species differs from that of *Paramys* by having the masseteric fossa bounded by much heavier ridges and terminating more anteriorly on the side of the mandible. This same effect of "incipient hystricognathy" is as strong on sciuravids and manitshine ischyromyids for the same reasons. In some instances the presence of a heavy chin process enhances a groove visible on the ventral side of the mandible which has been confused with the groove for the *masseter superficialis pars reflexus deep* on the ventral side of the mandible in truly hystricoganthous rodents (Woods, 1972).

Black and Stephens (1973) described the mandible of *Guanajuatomys* from Mexico as being hystricognathous. The angle of this mandible, however, is not laterally displaced from the plane of the horizontal ramus, and the mandible should not be considered hystricognathous.

The late Eocene rodent *Protoptychus* (Scott, 1895; Wilson, 1937) is fully hystricomorphous (Wahlert, 1973). Though the mandible of *Protoptychus* has not been fully described, Wahlert (1973), based on a personal communication from W. Turnbull, stated that *Protoptychus* was fully hystricognathous. This observation was followed by several authors (for example Wood, 1975; Dawson, 1977). However, more complete and fully prepared undescribed material of *Protoptychus* now available shows that the complete mandibles of *Protoptychus* are clearly sciurognathous.

Several mandibles of the cylindrodont *Mysops* from the middle Eocene are present in the collections of the USNM. None of the specimens that preserve the mandibluar angle are hystricognathous. Early Oligocene cylindrodonts have a mandible similar to those of reithroparamyines and are not hystricognathous.

The type specimen of *Prolapsus sibelatoris* (TMM 41372-179) is not fully hystricognathous jaw as stated by Wood (1972, 1973). The angle of the mandible of *Prolapsus* is no more laterally displaced than that of the early Eocene sciuravid *Knightomys* Gazin (1961). The mandible of *Prolapsus* is very robust and the breadth of the mandible is much greater than that of *Knightomys,* making the angle look more laterally displaced. Wood (1977, 1981) also stated that the skull of *Prolapsus* was hystricomorphous. However, the undescribed skull of *Prolapsus* on which Wood based his statement has been examined and compared to the skull of Bridgerian *Sciuravus.* The infraorbital foramina of these two genera are the same relative size and are clearly protrogomorphous.

Wood (1975) also noted that a small fossa on the lateral side of the mandible just ventral and posterior to the condyle of some franimorphs was for the attachment of the *masseter lateralis profundus pars posterior deep,* a muscle unique to hystricognathous rodents (Woods, 1972). Other than in the hystricognathous rodents and some "franimorphs," Wood (1975) found this fossa in the Oligocene sciuromorphous *Eutypomys.* This small fossa is also present in all manitshines, "*Leptotomus*" *costilloi,* and *Paramys copei,* all of which are ischyromyids. Whether or not it housed the attachment of this muscle cannot be determined, but clearly this feature cannot be used to relate the "franimorphs" to later hystricognathous rodents.

The "incipiently hystricognathous" condition in some early ischyromyids and sciuravids noted by Wood (1962, 1973, 1975) appears to be more common among early rodents than not, and may represent the primitive condition in rodents. Landry (1957:83), the first to suggest this hypothesis, stated, "It therefore seems that the most primitive ischyromyids have a jaw angle which shared the features of both Hystricognathi and Sciurognathi and which could have been the kind of structure possessed by their common ancestor."

In all, no specimens in the "Franimorpha" possess a definitely hystricognathous mandible. The Reithroparamyidae (Wood, 1981) should be returned to the subfamilial level under the Ischyromyidae. *Prolapsus* should be included as a member of the Sciuravidae. *Protoptychus* is unique among Eocene rodents and is best maintained in its own family Protoptychidae (see Simpson, 1945; Wilson, 1949). *Guanajuatomys* cannot be readily referred to any existing family of rodents, and is best maintained as Family *insertae sedis.*

Family Ischyromyidae Alston, 1876

Discussion.—A great deal of discussion has been concerned with the composition of the Ischyromyidae (Black, 1968*a,* 1971; Wood, 1976*a*). Here, the Ischyromyidae will include the "Paramyidae" of Miller and Gidley (1918) and Wood (1962) as a subfamily (or subfamilies) of the Ischyromidae. The differences between *Ischyromys* and the "Paramyidae" cited by Wood (1976*a*) are mainly concerned with the attachment of the masseter muscle on the skull. This difference is not significant enough to establish two distinct families for obviously closely allied genera (Black, 1968*a,* 1971). Black's (1971) diagnosis of the Ischyromyidae is accepted here.

Subfamily Paramyinae Simpson, 1941*b*

Diagnosis.—Medium to large sized rodents; skull with robust rostrum; nasal bones extend posteriorly on the skull far beyond the posterior extent of the premaxillaries; interparietal not present; auditory bulla not coosified with the skull; cheek teeth with simple pattern; P^4 submolariform and lacking a hypocone on all but the most primitive species; protoloph and metaloph more nearly parallel on upper molars; hypocone on upper molars usually small; anterior cingulum on lower molars continuous with metaconid and protoconid; mesoconids usually absent; entoconids generally continuous with posterolophids.

Tribe Paramyini, new rank

Diagnosis.—Medium sized paramyines; mandible intermediate in depth; lower incisors relatively narrow and flattened or convex anteriorly; cheek teeth distinctly cuspate; masseteric scar on mandible ends anteriorly below the M_2–M_3 boundary; posterior margin of the anterior root of the zygoma level with the posterior margin of P^4.

Included genera.—*Paramys* Leidy (1871), *Leptotomus* Matthew (1910), *Rapamys* Wilson (1940), *Thisbemys* Wood (1959*a*), *Uriscus* Wood (1962), *Hulgana* Dawson (1968*a*), and *Notoparamys,* new genus.

Comparison.—Paramyini differ from all reithroparamyines and ischyromyines by the lack of a hypocone on P^4; position of the anterior root of the zygoma and masseteric fossa on the mandible; having nasal bones extend farther posterior than the premaxillaries; lacking an interparietal bone on the skull; and generally having the entoconid continuous with the posteriolophid on the lower cheek teeth; and M^2 being longer than M^1 lingually. The Paramyini also differ from the Pseudoparamyinae and Ailuravinae by the lack of postorbital processes on the skull and having the nasal bones extending posterior to the premaxillary bones. The Paramyini are also generally larger than reithroparamyines.

The Paramyini can only be separated from the Manitshini by their smaller size and more cuspate cheek teeth. In manitshines the cheek teeth have shallow, nearly flat basins, and the cusps are marginal and less distinct. The skull and mandible of Paramyini are much more slender than in the Manitshini.

Paramys Leidy, 1871

Type species.—*Paramys delicatus* Leity, 1871.

Paramys copei Loomis, 1907

Plesiarctomys delicatissimus (Leidy) Cope, 1877, in part.
Paramys copei Loomis, 1907.
Paramys major Loomis, 1907.
Paramys primaevus Loomis, 1907.
Paramys quadratus Loomis, 1907.
Paramys bicuspis Loomis, 1907.
Paramys copei bicuspis Loomis, Wood, 1962.
Paramys copei major Loomis, Wood, 1962.

Type specimen.—AMNH 4755, skull and mandibles with some postcranial bones.

Horizon and locality.—Type and some referred specimens from type area of Lost Cabin Member, Wind River Formation, Wyoming. Other referred specimens from the Lysite Member, Wind River Formation; Debeque Formation, Colorado; Huerfano Formation, Colorado; Willwood Formation Wyoming; and San Jose Formation, New Mexico.

Age.—Early Eocene (Clarkforkian through Gardnerbuttean).

Referred specimens.—CM 19899, 19901, 9930, 20892, 21147–21150, 21168, 21170, 21172–21174, 21176–21178, 21180, 21181, 21218, 21227, 21934–21937, 21945, 22161–22167, 22169–22171, 22173, 22174, 22177, 22179, 22181–22203, 22204–22206, 22209, 22210, 22213, 22215, 22219, 22535, 22545, 22546, 22599, 22828, 22932–22934, 26509, 26513, 28711, 29160–29163, 30596, 30598, 31016, 35849–35857, 35864, 36495, 36496, 36498, 36500–36508, 36923–36926, 37165, 37171, 37177–37185, 38739, 38740, 4955 (from Lost Cabin Member, Wind River Formation).

CM 19894, 19895, 20888, 21899, 21913, 22820, 22821, 22822, 22824, 22825, 22830, 22832, 22834, 22838, 22846, 22880, 28706–28710, 28742, 28935, 29185, 35009–35014, 35016, 35017, 35028, 35031, 35032, 35926, 35933, 35935, 35936, 36085, 36087, 36088, 37077–37086, 38742, 38743, 38746–38756 (from Lysite Member, Wind River Formation).

CM 38757–38760 (from Almagre Member, San Jose Formation).

CM 38764 (from Largo Member, San Jose Formation).

CM 12006, 12008, 36116, 36256 (from Willwood Formation).

Also see Wood (1962:255–256) for referred material from other localities.

Discussion.—Loomis (1907) recognized seven species of *Paramys* from the early Eocene. Matthew (1910), in his review of the Ischyromyidae, recognized all of Loomis' species and included *Paramys buccatus* (Cope, 1877) from the early Eocene of New Mexico. Matthew (1910) divided the early Eocene *Paramys* species into three separate groups, the *P. buccatus* group (including *P. buccatus* and *P. atwateri*), the *P. primaevus* group (including *P. primaevus, P. excavatus, P. quadratus,* and *P. major*), and the *P. delicatus* group (including *P. copei, P. bicuspis,* and the Bridgerian species of *Paramys*).

Later, Matthew (1918) recognized only five early Eocene species of *Paramys,* synonymizing *P. primaevus* and *P. bicuspis* with *P. copei,* and allocating *P. quadratus* to a subspecies of *P. major.* Matthew did not discuss his earlier groupings of the species of *Paramys.*

The next major review of *Paramys* was by Wood (1962), who synonymized Loomis' (1907) *P. primaevus, P. quadratus, P. major,* and *P. bicuspis* under *P. copei,* recognizing *P. major* and *P. bicuspis* as subspecies. Wood followed Matthew (1910) in arranging species groups of *Paramys.* He included *P. copei* in a *P. delicatus* group along with the two Bridgerian species (*P. delicatus* and *P. delicatior*) and a new Wasatchian species *P. wortmani.*

Wood's (1962) overall synonymy of Loomis' species under *P. copei* is accepted here. His subspecific assignments cannot, however, be substantiated. The characters used by Wood (1962) to identify the subspecies of *P. copei* (incisor shape, size, shape of the mesostyle on the upper molars) are only minor variations within the range of variation of a single population. In many areas (for example, the Wind River Basin, Bighorn Basin, and Debeque Formation) as many as all three subspecies are recognized from the same level. This common occurrence and overlap of diagnostic characters seems to indicate that only a single species is present in all of these areas.

Guthrie (1971) synonymized *Paramys wortmani* Wood (1962) and specimens referred by Wood to *Thisbemys perditus* from the Lost Cabin Member, Wind River Formation with *P. copei. Paramys wortmani* is clearly distinct from *P. copei* and referred below to *Mytonomys* on the basis of a newly discovered maxillary fragment. The sample of *T. perditus* identified by Wood (1962) from Lost Cabin are all specimens in his private collection (labelled AEW) and appear from the figures to be some specimens of *P. copei* as well as specimens of *P. excavatus.*

Rose (1918) referred a few isolated upper incisors from the Clarkforkian of the Bighorn Basin to *Paramys* cf. *excavatus.* He noted that these incisors were markedly larger than those of *P. excavatus,* but that the lower dentitions referred to this species were near the size of *P. excavatus taurus* Wood (1962). The isolated upper incisors referred by Rose (1981) to *P.* cf. *excavatus* do not appear to be referable to *P. excavatus,* but more nearly approach *P. copei* or *Franimys amherstensis* in size. These specimens are longer anteroposteriorly than any specimens of *P. copei* (see Wood, 1962: Tables 9, 11, 13; Guthrie, 1967: Table 12; Rose, 1981). However, the single I^1 figured by Rose (1981: Fig. 64), according to the scale given on the illustration, is anteroposteriorly shorter than any of the measurements given by Rose for I^1 and well within the range of *P. copei* or *F. amherstensis.* This discrepancy in measurements may be due to the fact that Rose measured the length along the wear surface as opposed to the shortest anteroposterior diameter of the tooth.

These I^1's reported by Rose (1981) are here referred to *P. copei.* While these specimens are the same size as I^1 of *F. amherstensis,* enamel extends farther posteriorly on the medial side of the tooth as in *P. copei.* The rare occurrence of *P. copei* in the Clarkforkian is also true for the early Wasatchian levels in the Bighorn Basin.

Wood (1962) provided adequate figures of *P. copei.* Measurements of *P. copei* are provided by Wood (1962: Tables 8–13) and Guthrie (1967: Table 12; 1971: Tables 15, 18).

Wood's (1962) species groups of *Paramys* included the *P. delicatus* group (mentioned above) and a second group, the *P. excavatus* group which included *P. atavus, P. francesi, P. huerfanensis,* and the European species *P. teilhardi.* These species groupings appear somewhat artificial. The only feature that unites the species in each group is size, the *P. delicatus* group species being larger, and the *P. excavatus* group species, smaller. All of the species included in Wood's *P. excavatus* species group are referable to other genera, except *P. excavatus* (see Michaux, 1964; and later discussion this paper).

No species groups are recognizable within *Paramys.* This genus is composed of several distinct species that cannot be grouped into any category other than species.

Paramys excavatus Loomis, 1907
(Fig. 1)

Paramys excavatus Loomis, 1907.
Franimys lysitensis Guthrie, 1967.

Type specimen.—ACM 327, right mandible with M_1–M_3 and partial P_4.

Horizon and locality.—Type and some referred specimens from the type area of Lysite Member, Wind River Formation, Wyoming. Other referred material from the Debeque Formation, Colorado; Knight Member, Wasatch Formation, Wyoming; Lower Huerfano Formation, Colorado; Lost Cabin Member, Wind River Formation, Wyoming; and Almagre Member, San Jose Formation, New Mexico.

Age.—Middle early Eocene (Lysitean to Lostcabinian).

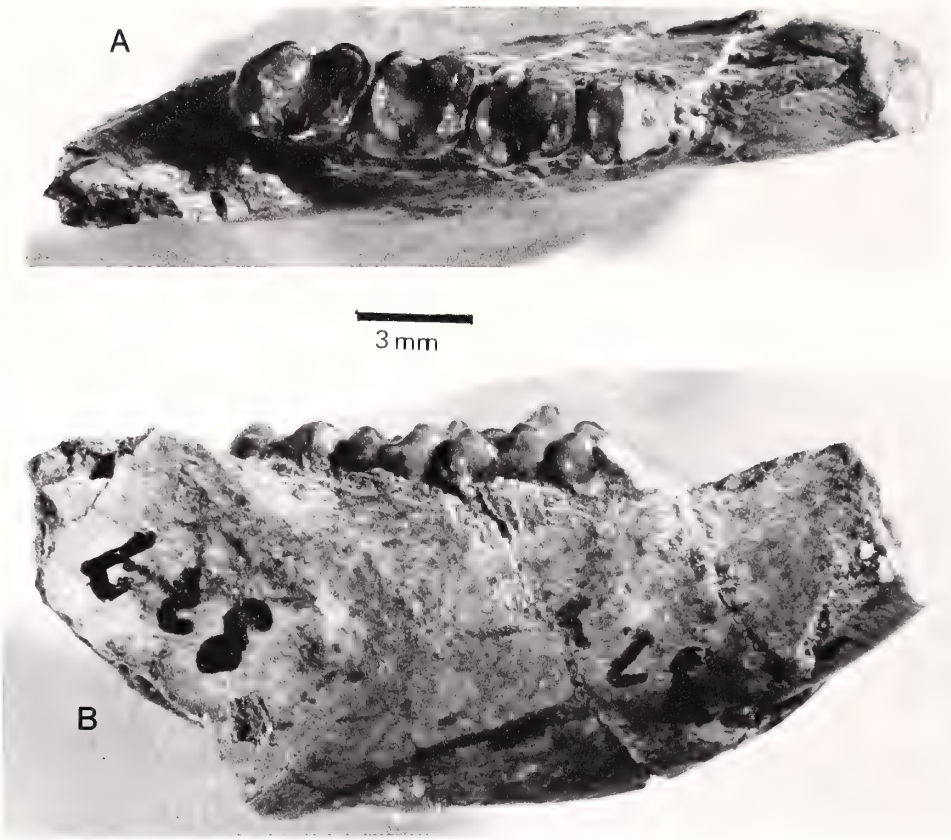


Fig. 1.—Holotype of *Paramys excavatus,* ACM 327. A) Occlusal view of P_4 (part)–M_3. B) Lateral veiw of mandible.

Referred specimens.—CM 21179, 22211, 22212, 22214, 22216, 22217, 22218, 22220, 22922, 26520, 31333, 35858, 36497, 37168, 37174, (from Lost Cabin Member, Wind River Formation).

CM 19893, 22853, 28705, 35029, 35030, 35934, 37090, 37092 (from Lysite Member, Wind River Formation).

CM 38761 (from Almagre Member, San Jose Formation).

CM 19540 (from Lower Huerfano Formation, locality VI).

Also see Wood (1962:256) for referred specimens from other areas.

Emended diagnosis.—Small species; enamel on lower molars smooth; lower molars nearly square in occlusal outline; P^4 anteroposteriorly compressed, lacking a protoconule and hypocone.

Discussion.—Wood (1962) recognized four subspecies of *P. excavatus.* This species is here restricted to his *P. e. excavatus.* The remaining subspecies of *P. excavatus* are referred elsewhere and will be discussed in following sections.

A single lower jaw with P_4–M_3 (CM 19540) from the Lower Huerfano (locality VI, Robinson, 1966) is referable to *P. excavatus.* This species has previously not been reported from the Huerfano (Wood, 1962; Robinson, 1966). A specimen of *P. excavatus* is now also known from the Almagre Member of the San Jose Formation of New Mexico (CM 38761).

Franimys lysitensis was described by Guthrie (1967:27) as differing from *P. excavatus* in ". . . weakness of the mesostylid and the anterior cingulum, and in the indistinctness of the trigonid basin." Guthrie's type (ACM 2536) and referred specimens (ACM 4394) do not differ markedly from the type and referred material of *P. excavatus,* and *F. lysitensis* should be considered a junior synonym of *P. excavatus.*

Guthrie (1971) synonymized both *Reithroparamys atwateri* and *R. pattersoni* with *P. excavatus.* The two specimens referred by Wood (1962:135) to *R. pattersoni* from the type area of the Lost Cabin Member of the Wind River Formation are more likely referable to *P. copei.* However, the remainder of the hypodigm for *R. pattersoni* from the Debeque Formation of Colorado is clearly distinct from *Paramys* (see below discussion of *Acritoparamys pat-*

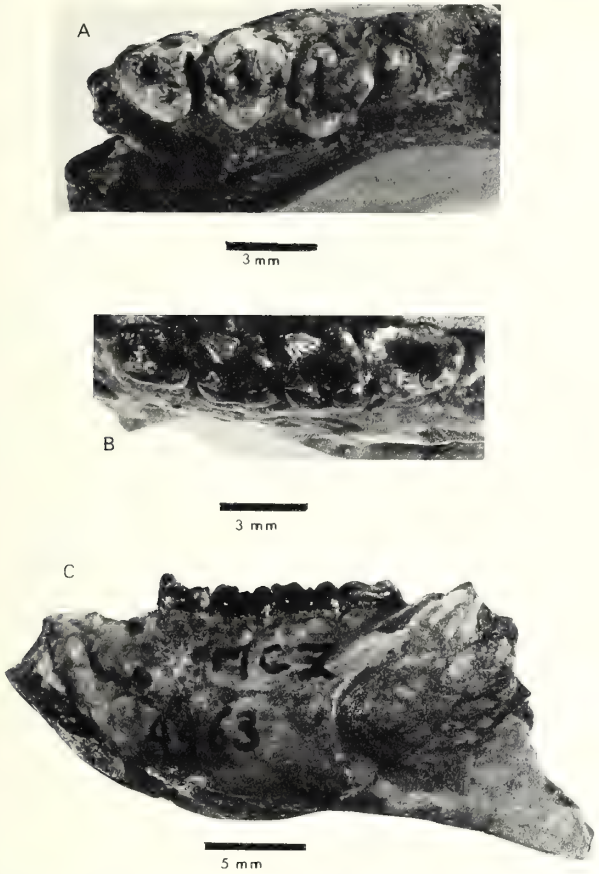


Fig. 2.—Upper and lower dentitions of *Paramys taurus.* A) RP^4–M^3, CM 12223. B) LP_4–M_3, MCZ 4463 (type). C) Lateral view of mandible, MCZ 4463.

tersoni). Likewise *R. atwateri* is also distinct from *P. excavatus* and should not be considered a synonym (see discussion of *A. atwateri*).

Dental measurements for *P. excavatus* were provided by Wood (1962: Tables 14, 15) and Guthrie (1967: Table 13; 1971: Table 16).

Paramys taurus Wood, 1962, new rank
(Fig. 2, Table 1)

Paramys excavatus taurus Wood, 1962.
Paramys excavatus obliquidens Wood, 1962.

Type specimen.—MCZ 4463, both mandibles with LP_4–M_3 and RM_1–M_3.

Horizon and locality.—Type from "1.7 miles west of Wardell's Lake, east of Tatman Mountain" (Wood, 1962:56), Willwood Formation, Wyoming. Referred specimens from elsewhere in the Willwood Formation and Four Mile Fauna, Wasatch Formation, Colorado.

Age.—Earliest Eocene (Clarkforkian to Graybullian).

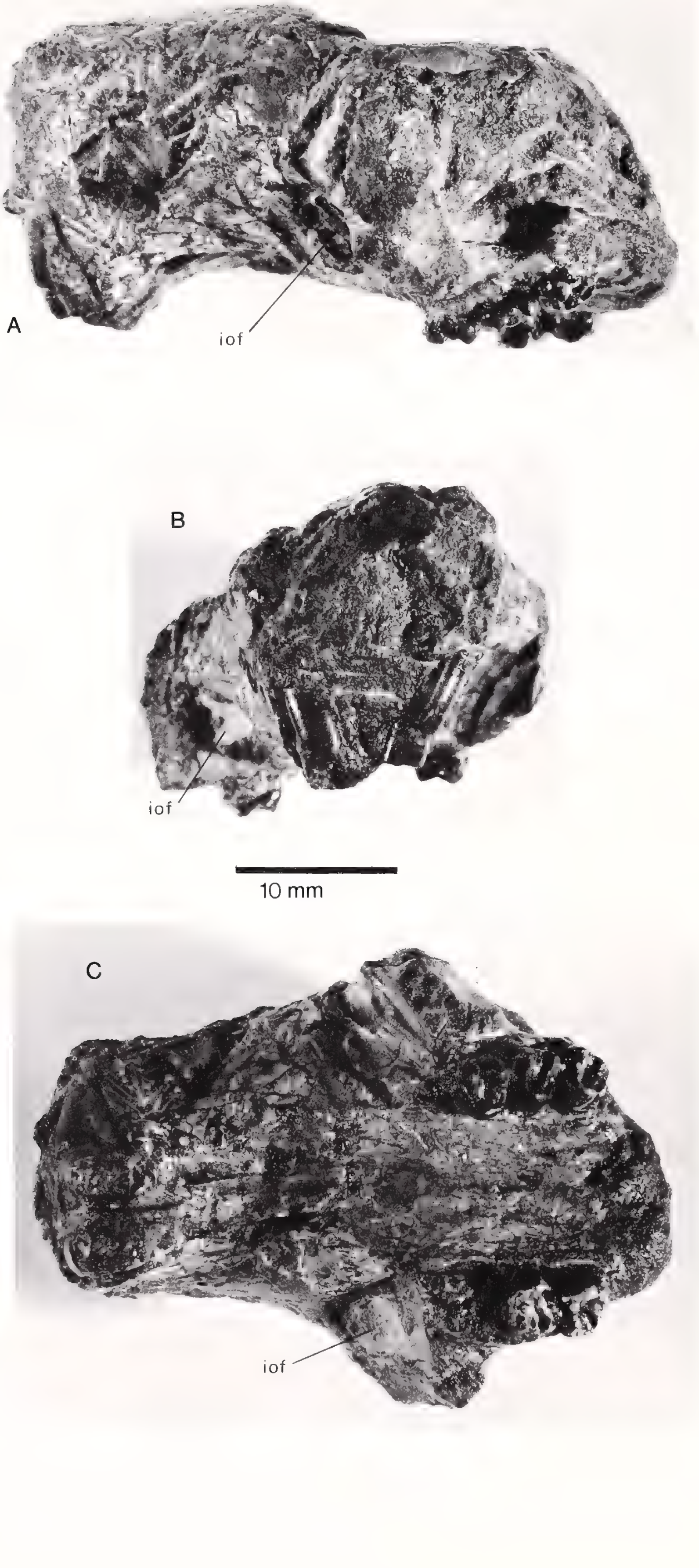
Referred specimens.—CM 12223, maxilla with P^4–M^3 from the Willwood Formation and several hundred isolated teeth from Sand and East Alheit Pocket Quarries, Four Mile fauna, Moffett County, Colorado (unnumbered AMNH specimens). Also see Wood (1962:58, 256) for total hypodigm.

Emended diagnosis.—Small species; lower molars rhomboidal in occlusal outline; hypoconulid variably present on P_4–M_2 which disappears with wear; P^4 anteroposteriorly compressed with protoconule and hypocone minute to absent.

Discussion.—Wood (1962) separated *P. excavatus taurus* from *P. e. obliquidens* on the basis of minor morphological differences of the molars and incisor, although these subspecies were of equal size and from the same levels of the Willwood Formation, Bighorn Basin, Wyoming. He stated that *P. e. obliquidens* had an I_1 with a concave anterior surface and a minor ridge running from the hypoconid toward the entoconid on the lower molars, not seen in *P. e. taurus.* The I_1 of the holotype of *P. e. obliquidens* (AMNH 16970) is not concave as figured by Wood (1962: Fig. 18p). The tooth appears flat anteriorly. The groove on the surface of I_1, if it were

Table 1.—*Dental measurements of* Paramys taurus, Paramys simpsoni, *and* Paramys nini. *Measurements in millimeters.*

Specimen no.	P^4			M^1			M^2			M^3	
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra
					Paramys taurus						
CM 12223	2.23	2.93	—	2.78	3.32	3.27	2.83	—	—	2.89	3.02
					Paramys simpsoni						
AMNH 80739 L	3.06	3.53	3.68	3.28	3.60	3.55	—	3.74	—	—	—
AMNH 80739 R	—	—	—	3.19	3.73	3.62	—	3.79	—	—	—
					Paramys nini						
YPM 14410 L	3.01	3.83	3.96	3.32	3.48	3.51	3.27	3.55	3.31	3.68	3.35
YPM 14410 R	—	—	—	3.35	3.50	3.22	—	—	—	—	—


A
iof
B
iof
10 mm
C
iof

truly concave, is so shallow that it is hardly detectable. The differences in the cross-sectional shape of I$_1$ of *P. e. taurus* and *P. e. obliquidens* are very slight and are no more different than variations accepted by Wood for other species of *Paramys.*

The minute ridge running from the hypoconid in *P. e. obliquidens* is only a minor crenulation on the enamel surface of the molars, and is equally as distinct in specimens of *P. e. taurus.* No differences exist between *P. e. obliquidens* and *P. e. taurus.* Therefore, they should be considered a single species that is distinct from *P. excavatus.*

Wood (1962: Fig. 18g) noted and figured a ridge extending into the talonid basin from the entoconid of P$_4$ on the type of *P. e. taurus.* This feature does not occur on the type (MCZ 4463) and cannot be considered a character of this species.

Paramys taurus is distinct from *P. excavatus* in having: 1) more rhomboidal shaped lower molars; 2) larger mesoconid; 3) a hypoconulid on the lower molars; and 4) minute hypocone generally present on P^4. These differences are consistent in all specimens referable to *P. taurus* and are distinct enough to warrant considering *P. taurus* as a separate species.

Wood (1962) stated that *P. e. obliquidens* (=*P. taurus*) was so close to *Reithroparamys atwateri* that he was tempted to put the subspecies in both *Paramys* and *Reithroparamys. Paramys taurus,* however, differs from *R. atwateri* in being larger with less distinct, more lingually placed hypoconulid on the lower molars; posteroloph continuous with the entoconid; and an accessory mental foramen only variably present on the mandible in differing positions. *Paramys taurus,* though similar in many features to *R. atwateri,* is clearly distinct from it.

A maxilla (CM 12223) with P^4–M^3 recovered from the Gray Bull level in the Bighorn Basin approaches the size of *P. taurus.* The molars are similar to those of *P. excavatus* and P^4 is anteroposteriorly compressed as in *P. excavatus* and *P. copei.* Several unnumbered isolated teeth are present in the Four Mile fauna (see McKenna, 1960). They are chiefly divisible into two species, *P. taurus* and "*R.*" *atwateri,* and are separable on the characters listed above. A number of specimens from the Bighorn Basin of *P. taurus* are being described elsewhere by T. Bown of the United States Geological Survey. Among these specimens there are some upper dentitions with P^4. A hypocone is only variably present on these specimens.

The three specimens of upper dentitions referred by Wood (1962) to *P. e. taurus* are disproportionately small relative to the known lower dentitions. (AMNH 15710 has been remeasured in Table 6, this paper). These specimens also differ from *P. taurus* in having P^4 not anteroposteriorly compressed with a distinct protoconule, anterior root of the zygoma level with the center of P^4, hypocone on M^1–M^2 larger in relation to the protocone, and and the protoloph and metaloph are less parallel converging toward the protocone. All of these features are characteristic of reithroparamyines. Thus, the three specimens of upper dentition referred by Wood to *P. e. taurus* should be referred to *R. atwateri,* which is known from the same localities of *P. taurus.*

The lower dentitions of "*Paramys* cf. *excavatus*" from the Clarkforkian of the Bighorn Basin (Rose, 1981) were described as being smaller than those of *P. e. taurus* from the early Wasatchian. However, only one specimen of Rose's "*P.* cf. *excavatus*" (UMMP 65117) is smaller than the ranges measured for *P. taurus* (including *P. e. obliquidens*) by Wood (1962: Tables 16 and 18). Only two measurements on UMMP 65117 (anteroposterior length of P$_4$, anterior width of M$_3$) are outside of the size range for *P. taurus.* The teeth of UMMP 65117 are so heavily worn that enamel has been lost on the lateral sides of the teeth and the anterior face of P$_4$, thus obscuring the true length and/or width of the teeth. The smaller size of this specimen of "*Paramys* cf. *excavatus*" can only be viewed as an effect of the wear of the teeth. Hence, the Clarkforkian specimens referred to this species are here allocated to *P. taurus* (see Wood, 1962: Tables 16, 18, for measurements of *P. taurus*).

Paramys simpsoni, new species

(Figs. 3, 4b, Table 1)

Type specimen.—AMNN 80739, partial skull with upper incisors and LP^4–M^2, RM^1–M^2.

Horizon and locality.—Locality 150 (Simpson, 1948), Largo Member, San Jose Formation, New Mexico.

←

Fig. 3.—Skull of *Paramys simpsoni,* AMNH 80739 (type). A) Lateral view. B) Anterior view. C) Ventral view. (iof = infraorbital foramen).

Age.—Middle or late early Eocene (Lysitean or Lostcabinian).

Hypodigm.—Type only.

Diagnosis.—Equal in size to *Paramys copei*; I^1 with narrow central groove; P^4 with large paracone which expands at the tooth anteriorly; P^4 with shortest (anteroposterior) length at the buccolingual center of the tooth; infraorbital foramen large for ischyromyid; maxillary-premaxillary suture on the side of the rostrum bends farther anterior than in *P. copei*; upper molars as in *P. copei.*

Etymology.—Patronym for George G. Simpson, who recovered the holotype.

Description.—In size and general shape, AMNH 80739 does not differ from *P. copei.* The posterior margin of the anterior root of the zygoma is in line with the anterior cingulum of M^1. The maxillary-premaxillary suture on the side of the snout is similar to that of *P. copei* but extends farther anteriorly. The infraorbital foramen is larger than in any other Eocene ischyromyid. It is evident on the specimen that preparation has somewhat altered the shape of the infraorbital foramen, but the true size of the foramen does not appear to have been affected.

A distinct groove is present on the anterior face of the upper incisors. P^4 is smaller than M^1, has a double metaconule, a large mesostyle with a low, short extension into the central basin, and lacks a hypocone. The posterior cingulum bends lingually at the posterolingual corner of the tooth. The paracone is more anteriorly placed than in P^4 of *P. copei* and slightly lingual to the metacone, making the tooth much longer bucally than lingually. The shortest anteroposterior length of P^4 is at the center of the tooth giving the tooth an "hourglass" occlusal shape. The anterior cingulum runs from the buccal margin of the protocone to the level of the center of the paracone. The protoloph is low with a minute protoconule.

The hypocone on the molars is small. M^1 is longer buccally than in *P. copei,* but not beyond the range of variation for that species. In all other features of the molars, *P. simpsoni* is similar to *P. copei.*

Discussion.—The size of the infraorbital foramen and distinct groove on the upper incisors of AMNH 80739 are unique for any species of *Paramys,* although in size and morphology of the molars *P. simpsoni* is identical to *P. copei.* Other features that separate *P. simpsoni* from *P. copei* are the morphology of P^4 and the pattern of the maxillary-premaxillary suture on the lateral side of the snout.

Several species of paramyines have been reported as having a shallow sulcus on the lower incisor (see Wood, 1962). This character is almost always variable when present. No upper incisors of *Paramys* are known to be sulcate. Only two ischyromyids are known to have a central groove on the upper incisor, *Reithroparamys delicatissimus* and "*Leptotomus*" *sciuroides.* Wood (1962) assigned an isolated upper incisor with a central groove to *Leptotomus* (=*Tapomys*) *tapensis* but its reference is uncertain. *Leptotomus bridgerensis* is known to have sulcate upper incisors but each incisor has two very broad, shallow grooves, unlike *P. simpsoni.* The groove in the I^1 of *R. delicatissimus* and "*L.*" *sciuroides* are also broader than that in I^1 of *P. simpsoni.*

There is no indication that a groove in the upper incisor is a variable character in paramyines. However, so few associated upper incisors are known that it is practically impossible to check at this time.

There is no indication that the infraorbital foramen of *P. simpsoni* has been invaded by a branch of the masseter muscle, though this foramen is clearly larger than in any other Eocene ischyromyid. It is difficult to base a new genus on *P. simpsoni* because it cannot be determined whether or not some of the characteristic features (sulcate I^1, enlarged infraorbital foramen, premaxillary-maxillary suture pattern) are just minor variations within a single genus or not. If more specimens referable to this taxon can be recovered, and these characteristics can be shown to be consistently different from those of *Paramys, P. simpsoni* may be distinct enough to warrant establishing a new genus of paramyine.

Paramys nini (Wood, 1962)
(Fig. 4a, Table 1)

Thisbemys nini Wood, 1962.

Type specimen.—YPM 14410, partial skull with RP^4–M^2 and LP^4–M^3.

Horizon and locality.—Head of Govilan Arroyo, Largo Member, San Jose Formation, New Mexico.

Age.—Middle early Eocene (Lysitean or Lostcabinian).

Emended diagnosis.—Intermediate sized species of *Paramys*; P^4 larger than M^1 with distinct hypocone; multiple mesostyles on upper cheek teeth; M^3 elongate posteriorly.

Discussion.—In the original description, Wood (1962) included the holotype from New Mexico and several referred specimens from the Huerfano Formation in the hypodigm of *Thisbemys nini.* All of the referred specimens are here allocated to *T. perditus* (see discussion below of *T. perditus*), making the holotype the only known specimen of the species.

Wood (1962) noted that the crenulations of the tooth enamel on the molars of *T. nini* were of a nature different from those of other species of *Thisbemys,* but maintained it in the genus. The crenulations on the cheek teeth of the holotype of *Para-*

mys nini are limited to the mesostylar area, and merely represent multiple mesostyles, a character common also in many specimens of *P. copei.* Both P^4 and M^1 of *P. nini* have a buccolingually elongate mesostyle which is larger than any of the other minute mesostyles on the teeth. Other than the elongate mesostyle, there is virtually no wrinkling of the enamel beyond that visible in those of other species of *Paramys.*

As noted by Wood (1962) the P^4 of *P. nini* is quite large relative to M^1, and M^3 is slightly more expanded posteriorly than in *P. copei.* It is difficult to determine whether or not the expansion of M^3 of YPM 14410 (type of *P. nini*) is truly distinct because M^3 is quite variable in most Eocene rodents, and the difference in *P. nini* is so slight it might well be within the bounds of variation for *P. copei.* P^4 of *P. nini* is distinct from that of any other species of *Paramys* in being wider than M^1 and having a hypocone. P^4 of *P. nini* is more molariform than that of *P. taurus,* which is the only other species of *Paramys* to possess a hypocone on P^4. The hypocone of P^4 of *P. nini* is very closely appressed to the protocone and separated from it only by a shallow groove. There is no groove separating the protocone from the hypocone and the lingual wall of the tooth as in the molars, thus, it appears that after moderate wear the hypocone would be indistinguishable from the protocone.

YPM 14410 is nearly identical to the holotype of *P. copei* (AMNH 4755) in size and all features of the skull that can be observed. The upper incisors and M^1–M^2 are also nearly identical to those of *P. copei.* M^1 of *P. nini* is slightly longer anteroposteriorly than in *P. copei,* but has the same proportions as M^1 in the skull described above of *P. simpsoni.*

Three skulls of *Paramys* are known from the Largo Member of the San Jose Formation of New Mexico, *P. copei* (CM 38764), *P. simpsoni* (AMNH 80739), and *P. nini* (YPM 14410). These skulls are all nearly identical in size and morphology of the upper molars. The major difference between them is the morphology of P^4. There are no known lower dentitions of appropriate size to be referred to these species from the Largo of New Mexico.

The morphology of P^4 of *Paramys nini* more closely approaches that of the Bridgerian species *P. delicatus* than does that of any other early Eocene species. *Paramys copei, P. excavatus* and *P. taurus* have a relatively short and wide P^4 that tapers lingually with a reduced protoloph and minute to absent protoconule. Both *P. nini* and *P. delicatus* have a longer, more molariform P^4 that is more nearly square in occlusal outline. The holotype of *P. copei* has a P^4 that approaches the shape of P^4 of *Leptotomus* (Wood, 1962). This is also true of P^4 of *P. excavatus* which is very similar to that of *P. copei.* Bridgerian *Leptotomus* could easily have been derived from either *P. copei* or *P. excavatus.*

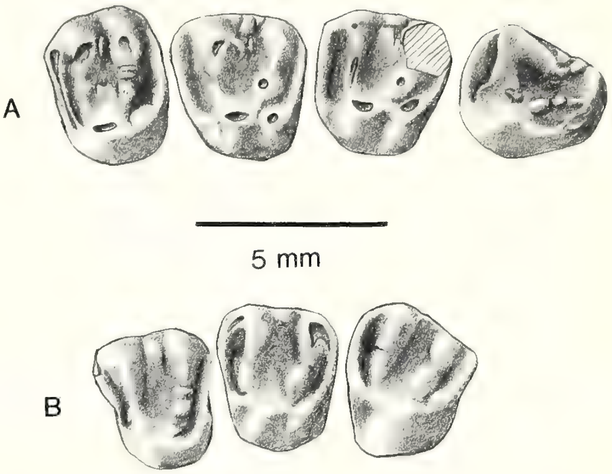


Fig. 4.—Upper cheek teeth of *Paramys nini* and *P. simpsoni.* A) *P. nini,* LP^4–M^3, YPM 14410 (type). B) *P. simpsoni,* LP^4–M^2, AMNH 80739 (type).

The only change in the dentition of *P. nini* needed to produce the morphology of *P. delicatus* is the full fusion of the hypocone with the protocone on P^4 which has been nearly completed in *P. nini,* and an increase in the rugosity of the enamel on the cheek teeth, which is probably foreshadowed in *P. nini* by the multiple mesostyles on the upper molars.

Thisbemys Wood, 1959*a*

Type species.—Thisbemys corrugatus Wood, 1959*a.*

Thisbemys perditus Wood, 1962
(Table 2)

Paramys excavatus gardneri Wood, 1962.
Leptotomus huerfanensis Wood, 1962.
Thisbemys nini Wood, 1962 (in part).
Paramys near *P. excavatus* West, 1973.

Type specimen.—FMNH P 26897, right mandible with M_2–M_3.

Horizon and locality.—Type from "southwest of Nipple Hollow, about eight miles southwest of Rifle, Colorado" (Wood, 1962:106), Lost Cabin level, Debeque Formation, Colorado. Referred specimens also from Lost Cabin level, Debeque Formation and

Table 2.—*Dental measurements of* Thisbemys perditus. *(compiled from Wood, 1962, Tables 19, 20, 27, 37, 38, 39, 40.) Measurements in millimeters.*

Measurements		N	M	OR
P_4–M_3		9	13.57	12.7–14.65
P_4	a–p	17	3.14	2.84–3.45
	tra	13	2.48	2.27–2.50
	trp	15	2.88	2.55–3.14
M_1	a–p	25	3.04	2.81–3.30
	tra	23	2.75	2.52–3.35
	trp	23	3.02	2.84–3.28
M_2	a–p	24	3.19	2.80–3.42
	tra	19	3.15	2.90–3.51
	trp	21	3.20	2.97–3.60
M_3	a–p	19	3.70	3.10–4.05
	tra	16	3.05	2.78–3.31
	trp	18	2.97	2.63–3.32
I_1	a–p	19	3.75	3.17–4.65
	tra	25	2.37	2.78–3.05
P^4	a–p	2	2.71	2.70–2.72
	tra	2	3.37	3.30–3.43
	trp	2	3.38	3.30–3.45
M^1	a–p	5	3.05	2.84–3.24
	tra	5	3.68	3.53–3.90
	trp	5	3.47	3.33–3.55
M^2	a–p	3	3.18	3.00–3.29
	tra	3	3.63	3.58–3.67
	trp	3	3.32	3.18–3.42
M^3	a–p	2	3.41	3.20–3.63
	tra	2	3.36	3.20–3.52
	trp	2	3.34	3.06–3.61

Upper and Lower Huerfano Formation, Colorado; Cathedral Bluffs Tongue, Wasatch Formation, Wyoming; and possibly the Bridger Formation, Wyoming.

Age.—Late early Eocene to possibly early middle Eocene (Lostcabinian-Gardnerbuttean, and possibly early Bridgerian).

Referred specimens.—FMNH PM 1214-PM 1219 (from Lost Cabin equivalent, Debeque Formation).

AMNH 17545 (from Lower Huerfano Formation, locality VI).

AMNH 17024, 17026, 17451, 17454, 17458, 17459, 17023, 55120, 55121, 55129, 55130, 55132, 55133, 55135, 55137–55139, 55141, 55143, 55146, 55150, 55193, 55196, 55197, 55199, 56542, and USNM 20136 (from the Upper Huerfano Formation).

UW 1363, 1367, 1370, and FMNH PM 15888, PM 15898, PM 21201, PM 21205–PM 21207, PM 21219, PM 21222 (from the Cathedral Bluffs Tongue, Wasatch Formation) and possibly FMNH PM 21076 (from Bridger Formation).

Discussion.—The size and morphology of the cheek teeth of *Thisbemys perditus* are the same as in *Leptotomus huerfanensis* and all specimens referred by Wood (1962) to *T. nini* except the holotype. There is no character that can be used to separate these species. Wood (1962: Fig. 30i) figured the cross-section of a lower incisor of *L. huerfanensis* that was similar to the incisor of other species of *Leptotomus*. However, the specimen figured by Wood, AMNH 55149, is from a mandible with I_1 and M_2 only. The molar in AMNH 55149 is identical to that of *Paramys copei* and should not be referred to the same species as the holotype of *L. huerfanensis*. The incisor in the holotype of *L. huerfanensis*, AMNH 55135, is only partially preserved but it is flattened anteriorly with enamel extending about half the dorsoventral height of the tooth on the lateral side. The widest part of the tooth is near its center. This tooth is the same as those figured by Wood (1962: Figs. 18q, 18r, and 37h, 37o) for *P. excavatus gardneri*, *T. perditus* and *T. nini*. The shallow groove on I_1 of *T. perditus* is variably present as in species of *Paramys*.

A previously undescribed maxilla with P^4–M^2 from the Upper Huerfano, AMNH 56542, has been identified in the AMNH collections as *Leptotomus huerfanensis*. This specimen shows irregularities in the enamel of the cheek teeth, P^4 without a hypocone, origin of the anterior root of the zygoma the same as in other paramyines, equivalent size to *T. perditus*, and is virtually identical to upper dentitions previously referred to *P. excavatus gardneri* and *T. perditus*. This specimen in no way resembles any species of *Leptotomus* except in features common to all paramyines. AMNH 56542 should be referred to *T. perditus*.

Specimens from the Cathedral Bluffs Tongue of the Wasatch Formation referred by West (1973) to *Paramys* near *P. excavatus* appear to be referable to *T. perditus*. Wood (1962) previously had cited a few specimens of *T. perditus* from the Cathedral Bluffs in the original hypodigm of the species. One specimen, P^4, from the Bridger Formation (FMNH PM 21076) was referred by West (1973) to *Paramys* near *P. excavatus* along with the specimens from Cathedral Bluffs. He noted that this specimen was identical to P^4 of *P. copei* or *P. excavatus* but was closer in size to the latter. Earlier, Wood (1959*a*) identified two isolated lower molars from Tabernacle Butte (Upper Bridger Formation) as *Paramys* cf. *excavatus*. These three specimens may represent a small Bridgerian species of *Paramys*, but the material is too poor to determine this at present.

Guthrie (1971) referred all of the specimens from

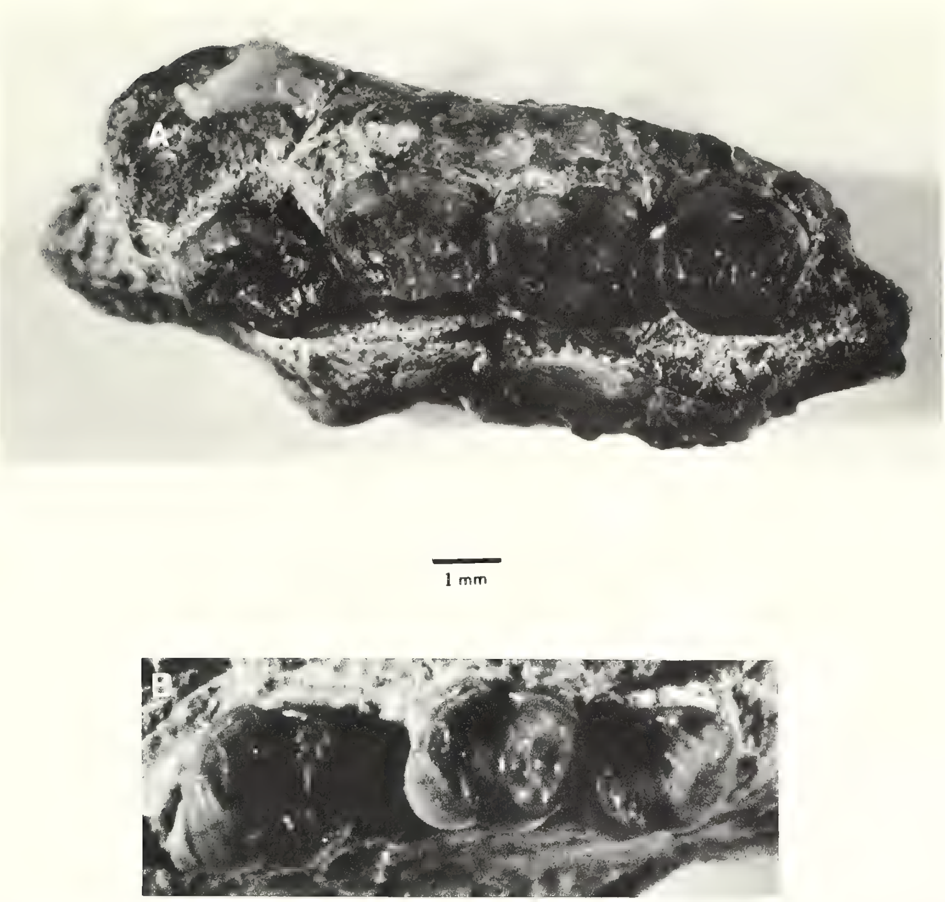


Fig. 5.—Dentition of *Thisbemys elachistos.* A) LP^4–M^3, AMNH 55122. B) RP_4–M_2, CU 23459 (type).

the Lost Cabin Member of the Wind River Formation identified by Wood (1962) as *T. perditus* to *Paramys copei.* There are no specimens in the extensive collections from the Wind River Basin at Carnegie Museum of Natural History that can be referred to *T. perditus.* The specimens figured by Wood from the Wind River Basin appear to be referable to either *P. excavatus* or *P. copei* in size and morphology (see Guthrie, 1971). None of the specimens referred to *T. nini* by Wood (1962) from the Upper Huerfano can be separated from *T. perditus.* The occurrence of *T. perditus* is thus limited to the Lost Cabin equivalent of the Debeque Formation, Huerfano Formation, Cathedral Bluffs Tongue, and possibly the Bridger Formation. Wood's (1962) identification of three different species of three genera from the Upper Huerfano, *Paramys excavatus gardneri, Leptotomus huerfanensis,* and *Thisbemys nini,* seems untenable and a single species, *Thisbemys perditus,* is here recognized in that unit.

Thisbemys elachistos, new species
(Fig. 5, Table 3)

Type specimen.—CU 23495, associated mandibles with LM_1–M_2 and RP_4–M_2.

Horizon and locality.—Locality II (see Robinson, 1966), Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Referred specimens.—CU 32161, RM_1–M_3; AMNH 55122, LP^4–M^3.

Diagnosis.—Smallest species of the genus; accessory lophs on cheek teeth broad and persistent until teeth heavily worn; P^4 nearly square in occlusal outline; M^3 also square with minute hypocone; masseteric fossa ends below anterior end of M_2.

Etymology.—*elachistos,* Greek, smallest.

Description.—P^4 is roughly square in occlusal outline. The protoloph is shorter than the metaloph. Both anterior and posterior cingula extend the entire width of the tooth. The metaconule is

Table 3.—*Dental measurements of* Thisbemys elachistos *and* Thisbemys *sp. Measurements in millimeters.*

Specimen no.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
					Thisbemys sp.							
PU 18418	—	—	—	—	—	3.46	3.63	3.46	—	4.13	3.46	—
					Thisbemys elachistos							
CU 23495 L	—	—	—	2.30	2.02	2.16	2.25	2.15	2.24	—	—	—
CU 23495 R	2.12	1.76	1.85	2.25	2.06	2.11	2.31	2.21	2.21	—	—	—
CU 32161 L	—	—	—	2.12	—	1.98	2.18	2.08	2.16	2.39	1.93	2.
CU 32161 R	—	—	—	2.12	1.83	2.02	2.17	2.12	2.15	2.29	1.95	1.
		P^4			M^1			M^2			M^3	
AMNH 55122	1.95	2.22	2.36	2.15	2.40	2.30	2.14	2.32	2.13	2.00	2.17	

large, nearly equal in size to the metacone. Accessory lophs running into the central basin of the tooth are short and broad. On the posterolingual corner of the tooth is a nearly circular wear facet. Anterior to it is a very narrow and shallow valley that separates it from a second nearly circular facet at the center of the lingual margin. Anterior to this second swelling at the anterolingual corner of the tooth is the protocone which is a larger wear facet with dentine exposed at its center. Neither of the two "cusps" posterior to the protocone appear to be homologous to the hypocone but are merely irregularities in the posterior cingulum.

M^1 and M^2 are nearly identical, and agree in general shape with those in other species of *Thisbemys.* The accessory lophs are short and broad as in P^4. M^3 is very close to M^2 in shape. The metacone is reduced to a small cuspule on the posterobuccal corner of the tooth, and the hypocone is just a minor swelling on the posterior cingulum. There is no posterior elongation or reduction of the hypocone area of this tooth.

I^1 is convex anteriorly with enamel extending half way up the lateral side of the tooth, and just slightly onto the medial side.

The masseteric fossa on the mandible extends anteriorly to below the posterior margin of M_1. There are two mental foramina on the mandible. A larger mental foramen is situated fairly low on the mandible, near mid-depth, and just anterior to P_4. A second, smaller foramen is lower on the mandible and beneath the posterior root of P_4.

P_4 is molariform but smaller than M_1. The metaconid is the largest cusp on the tooth. The trigonid basin is minute but present. The posterolophid is a broad continuous loph that runs from the hypoconid to the entoconid. Accessory lophs on P_4 are reduced to irregular swellings in the talonid basin.

The lower molars are rectangular in occlusal shape, increase in size posteriorly and do not differ markedly from those of *Thisbemys perditus.* The accessory lophs are short and broad but persist until the teeth are heavily worn. The lower incisor is parallel sided and flattened anteriorly on the holotype, and slightly concave anteriorly on the referred specimen. Enamel on the medial and lateral sides of the lower incisor is the same as for I^1.

Discussion.—Thisbemys elachistos is smaller than any other species of the genus. The nature of the accessory crenulations of the cheek teeth is similar to that of *T. perditus* in being low and relatively broad. P^4 of *T. elachistos* differs from that of all other species of *Thisbemys* in being more nearly square in occlusal outline.

Thisbemys elachistos and *T. perditus* are probably closely related and differ from all other *Thisbemys* in the number and nature of the accessory lophs or crenulations on the cheek teeth. All other species of *Thisbemys* have a network of fine crenulations on the cheek teeth. The condition in *T. elachistos* and *T. perditus* does not appear primitive for *Thisbemys,* but separately derived. The presence of an older species (described below but not named) that has irregularities of the enamel that approach the condition in other *Thisbemys* helps to support this suggestion.

Thisbemys sp.
(Fig. 6, Table 3)

Referred specimen.—PU 18418, right mandible with M_2–M_3 and talonid of M_1.

Horizon and locality.—Type area of the Lysite Member, Wind River Formation, Wyoming.

Age.—Middle early Eocene (Lysitean).

Description.—PU 18418 is equal in size to the Bridgerian *Thisbemys plicatus* and *T. corrugatus.* The masseteric fossa ends anteriorly below the posterior margin of M_2. The lower incisor is flattened medially and rounded anteriorly and laterally. Enamel extends only slightly onto the medial face of the incisor and about half way up the lateral face.

The occlusal pattern of M_2 and M_3 of PU 18418 does not differ from the basic paramyine pattern. Within the talonid basins of the molars are numerous small irregularities of the enamel. These irregularities are relatively small and low, possibly disappearing with heavier wear. The posterolophid is broken by a series of small narrow valleys, probably part of the system of irregularities of the enamel. These irregularities are isolated from one another and are not connected into elongate lophs or crenulations.

Discussion.—PU 18418 more closely resembles

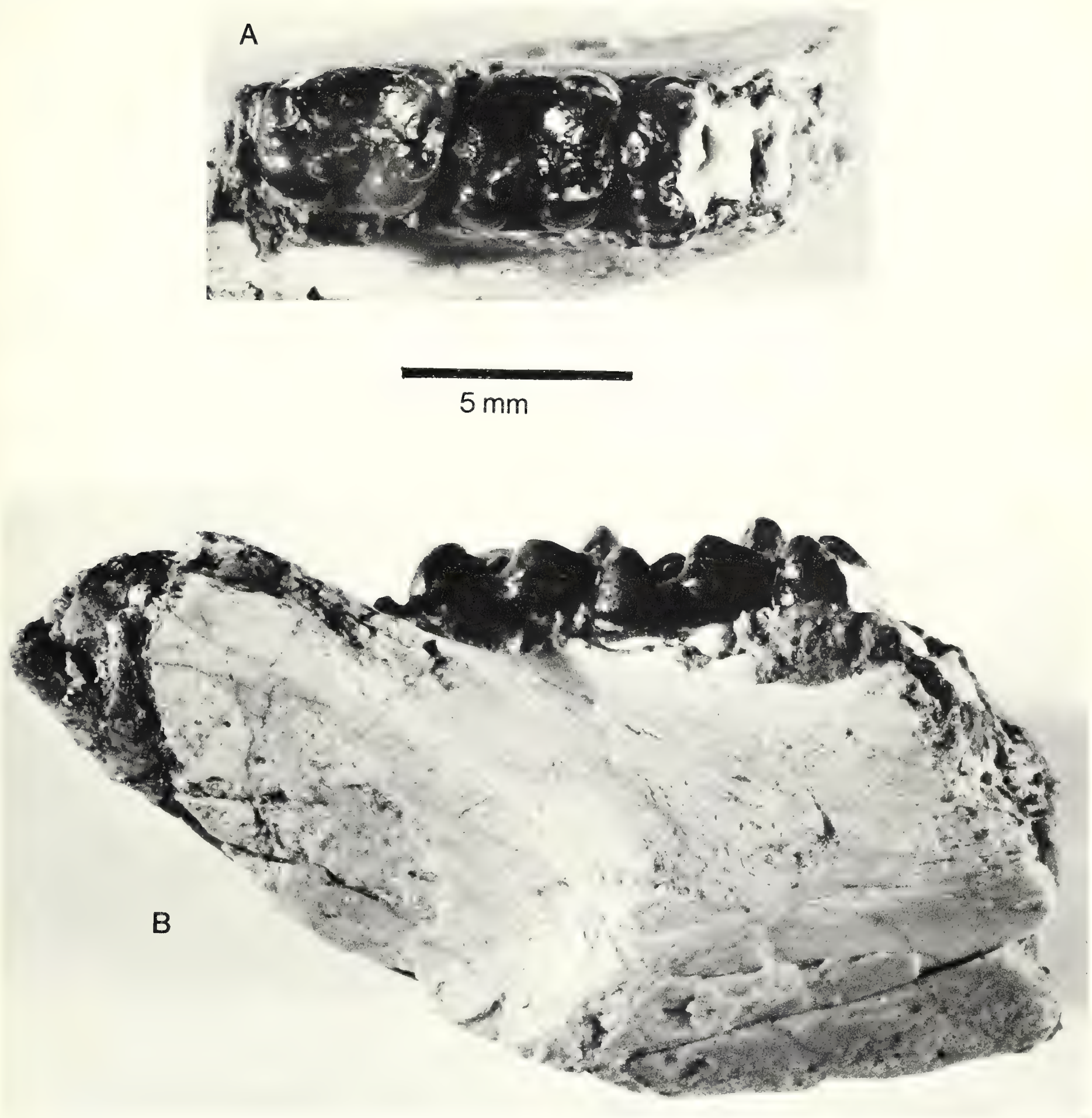


Fig. 6.—*Thisbemys* sp., M_1 (part)–M_3, PU 18418. A) Occlusal view. B) Lateral view of mandible.

the Bridgerian species *Thisbemys plicatus* and *T. corrugatus* than any other rodent. PU 18418 differs from these species in having less prominent irregularities of enamel in the basins of the lower molars that are not connected into minute crests.

There is nothing in the morphology of PU 18418 that would remove it from being a possible ancestor of *T. plicatus* or the later species of *Thisbemys.* The remaining early Eocene species of this genus, *T. perditus* and *T. elachistos,* represent a separate lineage from that represented by PU 18418 and the middle and late Eocene species of *Thisbemys.* Wood (1962) noted this same natural separation of *T. perditus* (and "*T. nini*") from the other species.

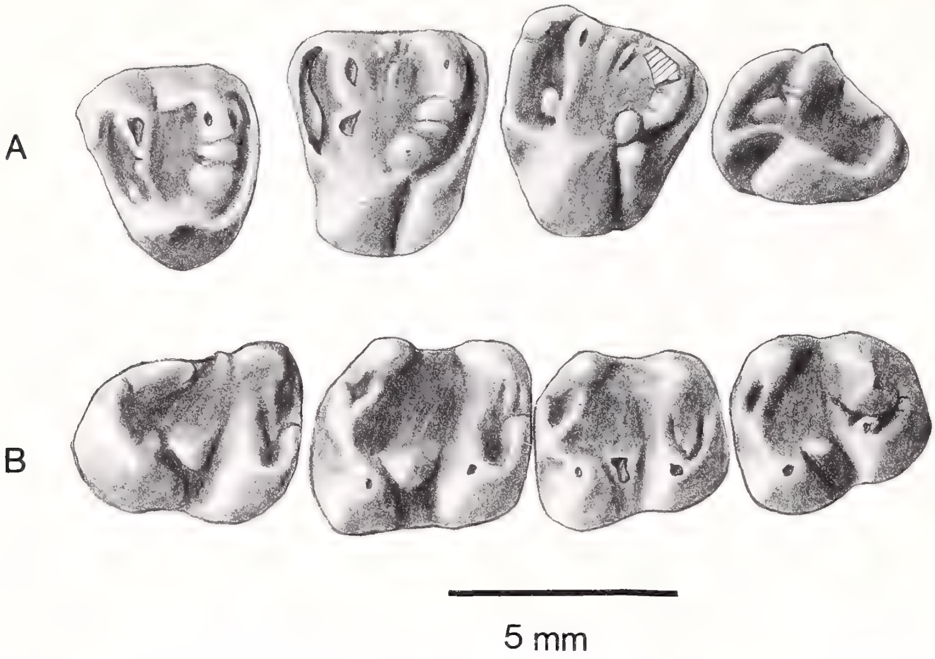


Fig. 7.—Cheek teeth of *Notoparamys costilloi.* A) LP^4–M^3, AMNH 55111 (type). B) RP_4–M_3, AMNH 55113.

Leptotomus Matthew, 1910

Type species.—Leptotomus leptodus (Cope, 1873).

Leptotomus cf. ***L. bridgerensis*** Wood, 1962

Referred specimen.—AMNH 55951, isolated LP^4 and LM^3.

Horizon and locality.—Locality III, Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Discussion.—Wood (1962) assigned two isolated teeth, P^4 and M^3 (AMNH 55951), from the upper Huerfano to *Leptotomus* cf. *L. parvus.* He recognized that the P^4 was distinct from that of *L. parvus,* but was of similar size.

AMNH 55951 is also very close to *L. bridgerensis* in size. The features of P^4 which distinguish AMNH 55951 from *L. parvus* (markedly tapered lingually, large mesostyle) are features of P^4 of *L. bridgerensis.* The P^4 of *L. parvus* is virtually inseparable from those of Bridgerian *Paramys,* as are the molars, suggesting that this species may well be referable to *Paramys* rather than *Leptotomus.*

Notoparamys, new genus

Type species.—Notoparamys costilloi (Wood, 1962).

Range.—Early Eocene of Colorado, New Mexico and possibly Wyoming.

Referred species.—Notoparamys arctios, new species.

Diagnosis.—P^4 submolariform but lacking hypocone; hypocone on M^1–M^2 distinct and buccally positioned adjacent to metaconule; M^3 small relative to M^1–M^2; mesoconid large on lower molars; hypoconulid on P_4–M_2 large, elongate transversely, lingually placed and connected to entoconid by two minute ridges originating from the lingual end of the hypoconulid; an accessory lophid runs buccally into the trigonid basin from the metaconid on the molars; I_1 is flattened medially and rounded laterally.

Etymology.—notos, Greek, southern; and *Paramys,* a closely related Eocene rodent.

Comparisons.—Notoparamys differs from other paramyines by the unique double attachment of the hypoconulid to the entoconid on the lower cheek teeth, cross-sectional shape of I_1, the deep groove separating the hypocone from the protocone on M^1–M^2, more buccal position of the hypocone on the upper molars, and larger mesoconid on the lower cheek teeth. *Notoparamys* also differs from *Thisbemys* in the fine crenulations present in the basins of the cheek teeth of the latter are not found on the former.

Notoparamys differs from *Rapamys* by the lack of enlarged metaconules on the upper cheek teeth, and from *Uriscus* by the occlusal outline of the lower molars. *Notoparamys* differs from all other ischyromyids by the characters listed above under the diagnosis of the Paramyini.

Notoparamys costilloi (Wood, 1962)
(Fig. 7)

Type specimen.—AMNH 55111, crushed skull with left and right P^4–M^3.

Horizon and locality.—Type and some referred specimens from locality VIII, Lower Huerfano Formation, Colorado. Other specimens from Almagre Member, San Jose Formation, New Mexico.

Age.—Late and possibly middle early Eocene (Lostcabinian and possibly Lysitean).

Referred specimens.—AMNH 55110, crushed skull; AMNH 55113, two complete mandibles (from Lower Huerfano); AMNH 80686, M^2; AMNH 80727a, I_1 (from Almagre Member, San Jose Formation).

Emended diagnosis.—Intermediate sized paramyine (see Wood, 1962: Tables 27, 28); metaconules doubled on P^4–M^2; low broad accessory lophs originate from the metaconid and protoconid and run into the trigonid basins of M_1–M_3; double lophs connecting the entoconid and hypoconulid relatively high, posterior loph broken at its center by narrow valley.

Discussion.—Wood (1962) first described *Leptotomus costilloi,* basing the generic reference on the cross-sectional shape of the lower incisor. Guthrie (1967) noted several differences in the dentition of *L. costilloi* from other species of *Leptotomus* but followed Wood's allocation because of the shape of the lower incisor. However, the I_1 of "*L.*" *costilloi* is quite distinct from that of species of *Leptotomus* such as *L. leptodus* and *L. bridgerensis* in being much broader, nearly circular in cross-section, enamel not extending as far posteriorly on the lateral surface, not having a narrow (nearly pointed) anterior face, and having its widest point near the center of the tooth.

The molars are equally distinct from those of *Leptotomus.* In the lower molars, the connection of the posterolophid to the entoconid, large isolated mesoconids, unique connection of the hypoconulid to the entoconid and larger trigonid basins filled with accessory lophids are not present in any species of *Leptotomus.* The upper cheek teeth of *Notoparamys costilloi* are also distinct from those of *Leptotomus* in the shape of the teeth and size and position of the hypocone on M^1–M^2. *Notoparamys costilloi* is not congeneric with *Leptotomus* and is unique among paramyines.

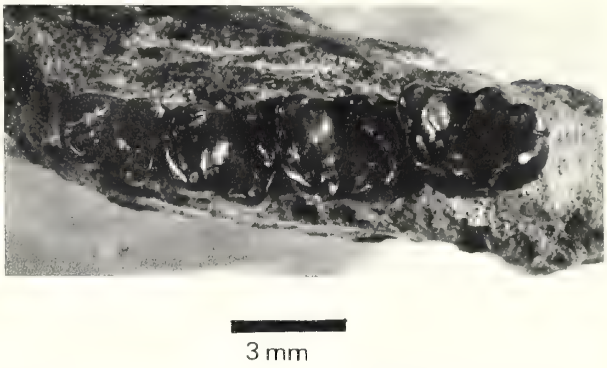


Fig. 8.—Holotype of *Notoparamys arctios,* FMNH P 26503, LP_4–M_3.

An isolated lower molar (AMNH 80686) and an I_1 (AMNH 89727a) from the Almagre Member of the San Jose Formation, New Mexico, closely resemble those of *N. costilloi.* the isolated M_2 is slightly smaller than the specimens from the Huerfano (Table 5). There are no accessory lophids filling the trigonid basin, and the minute valley between the double lophids that connect the entoconid and hypoconulid is less anteroposteriorly compressed. The lower incisor is identical to I_1 of *N. costilloi* from the Huerfano but is also slightly smaller (Table 5). These two specimens are referred to *Notoparamys* cf. *N. costilloi.*

A single M^1 (AMNH 4222g) from an unknown level in the Willwood Formation, Wyoming, also shows some similarities to *N. costilloi.* AMNH 4222g is slightly smaller than M^1 of *N. costilloi* from Colorado. The metaconule is buccolingually elongate but not multiple as in the Colorado material. All other features of AMNH 4222g agree with *N. costilloi.* This specimen is too large to be referred to the Lysitean species of *Notoparamys* (described below) and differs enough from *N. costilloi* that it may represent a new species. AMNH 4222g is here identified as *Notoparamys* sp.

Notoparamys arctios, new species
(Fig. 8, Table 4)

Reithroparamys debequensis Wood, 1962 (in part).

Type specimen.—FMNH P 26503, left mandible with P_4–M_3.

Horizon and locality.—Charard Park, "about five

Table 4.—*Dental measurements of* Notoparamys *(in millimeters).*

Measurements	*Notoparamys arctios* (FMNH P 26503)	*Notoparamys* cf. *N. costilloi* (AMNH 80686)	*Notoparamys* sp. (AMNH 4222g)
P_4–M_3	12.89		
P_4 a–p	2.67		
tra	2.02		
trp	2.32		
M_1 a–p	3.02	3.84	
tra	2.49	3.36	
trp	2.76	3.62	
M_2 a–p	3.09		
tra	2.84		
trp	2.93		
M_3 a–p	3.96		
tra	2.91		
trp	2.59		
M^1 a–p			3.61
tra			4.48
trp			4.11
		(AMNH 80727)	
I_1 a–p		3.16	
tra		2.16	

miles southwest of Rifle, Colorado" (Wood, 1962: 134), Lysite equivalent, Debeque Formation.

Age.—Middle early Eocene (Lysitean).

Hypodigm.—Type only.

Diagnosis.—Small species; no accessory ridge in the trigonid basin from the protoconid; parallel ridges connecting entoconid and hypoconulid minute and the posterior one not broken by narrow valley; I_1 more nearly parallel sided.

Etymology.—*arctios*, Greek, northern.

Description.—The mandible and lower teeth of *Notoparamys arctios* are quite similar to those of *N. costilloi* but are about one-third smaller. The cheek teeth of *N. arctios* have smaller mesoconids and hypoconulids, less bulbous cusps and weaker connections of the entoconid to the hypoconulid on the lower cheek teeth than in *N. costilloi.*

Both M_1 and M_2 of *N. arctios* have a low, broad loph running from the metaconid into the trigonid basin. This feature is much more pronounced in *N. costilloi.* Because the small lophs connecting the hypoconulid to the entoconid are much smaller on the molars of *N. arctios,* the small depression surrounded by these lophs is much shallower.

The trigonid of M_3 is relatively larger than in *N. costilloi* and lacks any accessory lophs within it. The hypoconulid on M_3 of *N. arctios* is separated from the entoconid by a distinct valley and forms a separate posterolingual lobe on the tooth.

The lower incisor is relatively broad, convex anteriorly and laterally, and flattened medially. The widest part of the incisor is at one-third the dorsoventral height of the tooth. Enamel extends laterally about half the dorsoventral height of the tooth, and just slightly onto the medial surface.

Discussion.—*Notoparamys arctios* differs from *N. costilloi* in its smaller size, less prominent cusps, weaker connection of the entoconid and hypoconulid, fewer accessory lophs in the trigonids of the molars, and shape of the lower incisor. In all these features *N. arctios* is more primitive than *N. costilloi.* There are no features of *N. arctios* that would remove it from an ancestral position to *N. costilloi. Notoparamys arctios* is also known from older levels (Lysitean) than *N. costilloi* (Lostcabinian).

The holotype of *N. arctios* cannot be referred to *Reithroparamys debequensis* as was originally done by Wood (1962). *Notoparamys arctios* is larger and the molars are relatively broader than *R. debequensis. Notoparamys arctios* also lacks the separation of the entoconid from the posterolophid on the molars and the associated partial hypolophid that are present in *R. debequensis.*

Tribe Manitshini Simpson, 1941*b*

Included genera.—*Manitsha* Simpson (1941*a*), *Pseudotomus* Cope (1872), *Ischyrotomus* Matthew (1910), and *Quadratomus,* new genus.

Discussion.—Simpson (1941*b*) originally included only the North American genera *Manitsha, Psueodtomus* and *Ischyrotomus* in the Manitshini. Wood (1962) raised the rank of the group to subfamily and included the European genus *Plesiarctomys.* Michaux (1968) included *Plesiarctomys* in the Pseudoparamyinae based predominantly on the lack of P^3. Wood (1970), in his review of the genus, included *Plesiarctomys* in the Manitshinae and pointed out that at least a dP^3 is present in most specimens of *Plesiarctomys* but later (Wood, 1976*a*) followed Michaux in including *Plesiarctomys* in the Pseudoparamyinae.

Even if *Plesiarctomys* possesses a P^3, all of its features shared with manitshines are allometric changes. All other features of *Plesiarctomys* agree with Michaux's (1964, 1968) definition of the Pseudoparamyinae.

The inclusion of *Quadratomus* does not alter Simpson's (1941*b*:142) diagnosis for the tribe except for the shape of the lower incisor and possession of a heavy chin process or "symphyseal flange" on the mandible.

Quadratomus, new genus

Type species.—*Quadratomus grandis* (Wood, 1962).

Range.—Late early Eocene of Colorado, middle Eocene of Wyoming, and possibly early Oligocene of Texas.

Referred species.—*Quadratomus* sp. and ?*Q. gigans* (Wood, 1974).

Diagnosis.—Anterior root of the zygoma arises buccal to M^1 and arches dorsally; masseteric fossa ends between M_2–M_3 on the mandible; lower incisor narrow anteriorly with small flat surface, greatest width posterior; upper molars nearly square in occlusal outline; lophs on the molars very low and broad, separated by a shallow broad central basin; hypocone small on upper molars; trigonid basins on lower molars anteroposteriorly compressed, closed anteriorly and nearly closed posteriorly by narrow ridges from the metaconid and protoconid; talonid basins broad and shallow; mesoconid minute; ectolophid absent; anterior and posterior transverse widths of the lower molars nearly equal; M_3 elongate; lower molars longer than wide; posterolophid continuous with entoconid on lower cheek teeth; no heavy chin process on the mandible.

Etymology.—*quadratos,* Latin, squared; *mus,* Latin, mouse.

Comparisons.—Though the morphology of the cheek teeth, general size and massiveness of the mandible, and modification of the ventral margin of the zygoma of *Quadratomus* make it referable to the Manitshini, it differs from all other manitshine genera in the shape of the lower incisor, lack of a heavy chin process on the mandible, position of the anterior root of the zygoma, and in having lower molars longer than wide.

Quadratomus grandis (Wood, 1962)
(Fig. 9)

Leptotomus grandis Wood, 1962

Type specimen.—USNM 10137, mandible with P_4–M_3, postcranial and skull fragments and I^1.

Horizon and locality.—Type and referred specimens from localities II and III, Upper Huerfano Formation, Colorado.

Age.—Latest early Eocene (Gardnerbuttean).

Referred specimens.—AMNH 17452, 17453, 17457, 55126, 55192.

Emended diagnosis.—Average size for a manitshine (see Wood, 1962: Tables 27, 28); minute irregularities on cheek teeth; I_1 may have anterior sulcus; mesoconids present on lower molars; posterior margin of anterior root of zygoma level with the paracone of M^1.

Discussion.—Wood (1962) thoroughly described *Leptotomus grandis.* No additional material has been found since that time so no further description is necessary.

Wood (1962) referred this species to the *Leptotomus,* as he did with *Notoparamys costilloi,* on the basis of the shape of the lower incisor, even though he noted the considerable difference between I_1 of *L. grandis* and other species of *Leptotomus.* I_1 of *Quadratomus grandis* is clearly distinct from that of *Leptotomus.* It is flattened and much broader anteriorly, not tapering anteriorly as markedly. The lower incisors of *Q. grandis* most closely resemble those of *Paramys delicatus,* except they are slightly narrower. The lower cheek teeth of *Q. grandis* are more similar to those of manitshines and differ from those of *Leptotomus* in having: 1) lower molars not lophate; 2) cusps more marginal and less distinct; 3) posterolophid connected to the entoconid; 4) trigonid basins more anteroposteriorly compressed; 5) enamel not smooth on cheek teeth; and 6) talonid basins large and shallow. The upper teeth differ from those of *Leptotomus* in having: 1) nearly square occlusal outline; 2) P^4 relatively longer; 3) protoloph and metaloph broadly separated, leaving shallow, broad trigon basin; and 4) less cingular development on the parastylar area. The maxilla of *Q. grandis* also differs from that of *Leptotomus* in the more posterior placement of the anterior root of the zygoma and the nearly vertical broad anterior face of the zygoma. The unusual ventral part of the anterior root of the zygoma noted by both Wood (1962) and Black (1971) arches dorsally. This arrangement of the zygoma is known elsewhere only in manitshines.

West (1973) referred a partial skeleton with all upper and lower teeth from the Bridger Formation to *Pseudotomus robustus.* This specimen, however, is clearly congeneric with *Q. grandis* and distinct from *Pseudotomus* and other manitshines in: 1) lower crowned cheek teeth; 2) trigonids on lower molars broader; 3) lower molars longer than wide; 4) I_1 narrow; 5) mandible more slender without heavy chin process; 6) upper molars much longer; and 7) anterior root of the zygoma more posteriorly positioned. The Bridgerian material represents a distinct species of *Quadratomus* that will be described elsewhere. The two specimens of *L. grandis* cited by Wood (1962) from the Bridger Formation are probably not referable to *Q. grandis,* and are within the size range of *L. bridgerensis.*

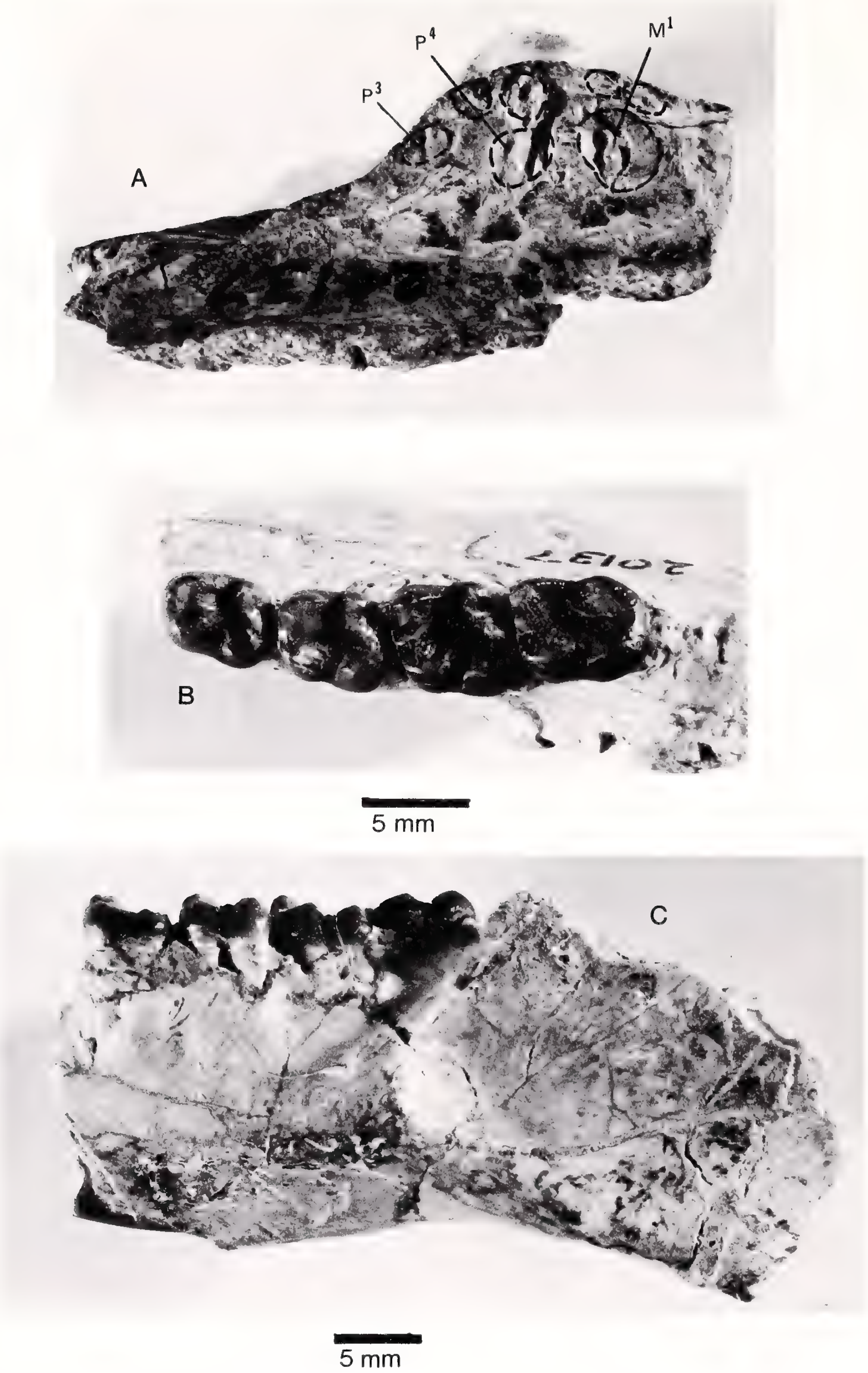


Fig. 9.—Holotype of *Quadratomus grandis,* USNM 20137. A) Ventral view of maxilla with alveoli for P^3–M^1. B) Occlusal view of LP_4–M_3. C) Lateral view of mandible.

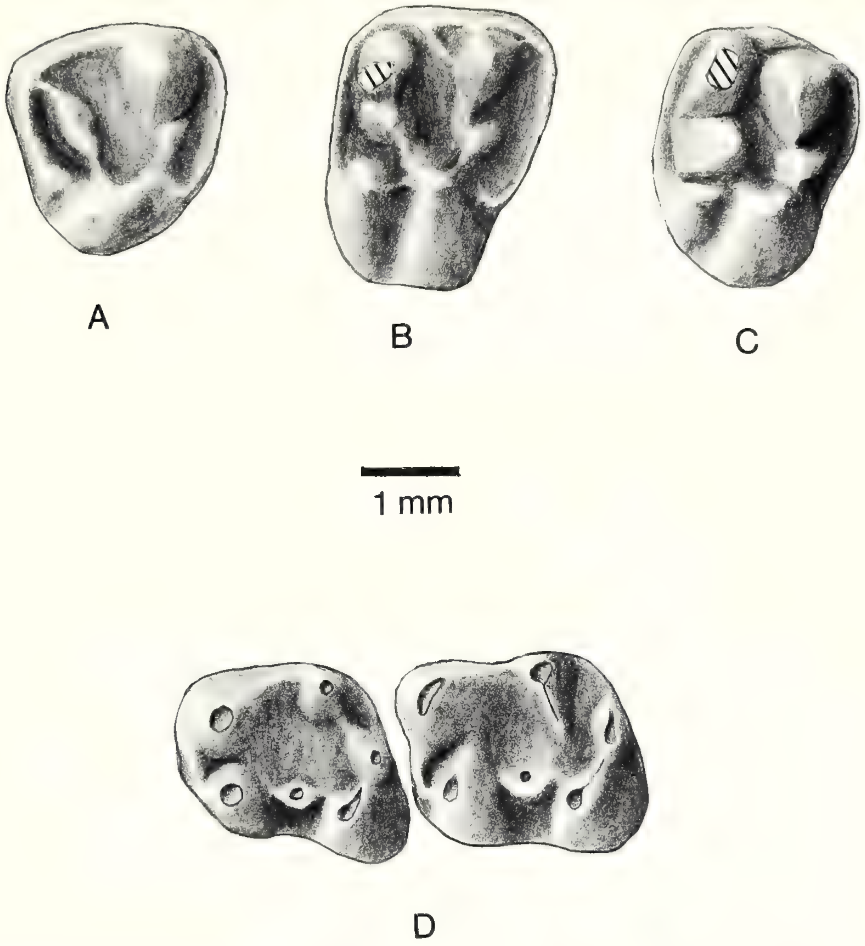


Fig. 10.—Cheek teeth of *Reithroparamys ctenodactylops.* A) RM^3, UW 15010. B) RM^1 or M^2, UW 15263. C) RP^4, UW 15262. D) LM_1–M_2, UW 15008 (holotype).

Wood (1974) described a large species, *Leptotomus gigans,* from the early Oligocene Vieja Group, Texas. This species, however, has a lower incisor that more nearly approaches that of *Quadratomus,* and molars that more closely resemble typical manitshines. The mandible of *L. gigans* is more slender than manitshines, and more similar to that of *Quadratomus.* The lower cheek teeth are low crowned, massive, and nearly square in occlusal outline as in *Quadratomus.* The occlusal pattern of the teeth of *L. gigans* differs from that of manitshines and *Quadratomus* in having a trigonid that is not as anteroposteriorly compressed. The partial hypolophid on the lower cheek teeth of *L. gigans* is not present in *Q. grandis* or the Bridgerian species of *Quadratomus* but a complete hypolophid is present in *Manitsha tanka.*

Overall, *Leptotomus gigans* more closely resembles *Quadratomus* than any other genus of ischyromyid, but cannot be definitely referred to this genus. Therefore, *L. gigans* is here questionably referred to *Quadratomus* as ?*Q. gigans.*

Simpson (1941*b*) viewed the members of the Manitshini as representing a single lineage leading to the Oligocene genus *Manitsha. Quadratomus* represents a separate lineage ending in the early Oligocene with ?*Q. gigans.*

Subfamily Reithroparamyinae Wood, 1962

Emended diagnosis.—Small to medium sized ischyromyids; auditory bulla large and coosified with the skull; posterior margin of nasal bones level with that of premaxillaries; posterior margin of anterior root of zygoma level with center of P^4 or farther anterior; incisors narrow; mandible slender; P^4 molariform with hypocone present; M^1 nearly equal in size and proportions to M^2; hypocones on upper molars relatively large; metaconid lingually positioned on M^1–M^2; entoconid separated from posterolophid; hypoconulid present on lower molars.

Included genera.—*Reithroparamys* Matthew (1920), *Microparamys* Wood (1959*a*), *Lophiparamys* Wood (1962), *Acritoparamys,* new genus, and possibly *Apatosciuravus,* new genus.

Comparisons.—The Reithroparamyinae differ from paramyines in having nasal bones extending posteriorly to the same level as the premaxillaries on the dorsal side of the skull, the anterior root of the zygoma and masseteric scar on the mandible anteriorly placed, and being generally smaller in size. They differ from paramyines, pseudoparamyines and manithines in having hypocone on P^4, relatively larger hypocone on M^1–M^2, isolated entoconid and larger hypoconulid on the lower molars, and having a bony auditory bulla attached to the skull. This last feature is only known for *Reithroparamys delicatissimus* and "*Paramys*" *sciuroides* Scott and Osborn (1887; not referable to *Leptotomus* but rather *Reithroparamys*) and may not be true for all reithroparamyines. The Reithroparamyinae differ from the Ischyromyinae by having lower crowned, less lophate teeth; and having a small infraorbital foramen with no associated modification of the zygomasseteric structure.

Discussion.—Originally, Wood (1962) included *Reithroparamys, Rapamys,* and his new genera *Franimys* and *Tapomys* in the Reithroparamyinae. One of the major characters uniting these genera was the possession of an "incipiently hystricognathous" mandible. Wood (1962) repeatedly compared the Reithroparamyinae with the early Oligocene hystricognathous rodent *Platypittamys* from South America. As discussed above, none of the reithroparamyines are hystricognathous or "incipiently hystricognathous," but are entirely sciurognathous and any similarities between them and early South American hystricognathous rodents are superficial.

Black (1971) was the only other author to diagnose the subfamilies of the Ischyromyidae. He referred *Rapamys* to the Paramyinae and included *Microparamys, Lophiparamys,* and the late Eocene *Janimus* in the Reithroparamyinae along with Wood's included genera. Black (1971) synonymized *Tapomys* under *Leptotomus,* which he included in the Paramyinae.

Wood's (1976*a*) later subfamilial arrangement was virtually identical to his first. He did not follow Black's (1971) synonymy of *Tapomys* and included *Janimus* in the Microparamyinae.

The classification followed here more closely follows that of Black (1971). *Franimys,* previously considered a reithroparamyine by both Black (1971) and Wood (1962, 1976*a*), appears more closely related to the European *Pseudoparamys* and is here placed in the Pseudoparamyinae of Michaux (1964). Both Dawson (1966, 1977) and Wood (1974) compared *Janimus* with early Oligocene *Eutypomys* and suggested a possible relationship. *Janimus* is here referred questionably to the Eutopomyidae.

Reithroparamys Matthew, 1920

Type species.—*Reithroparamys delicatissimus* (Leidy, 1871).

Reithroparamys ctenodactylops, new species

Type specimen.—UW 15008, partial left mandible with M_1–M_2.

Horizon and locality.—Type and all referred specimens from SW¼, NW¼, SW¼, sec. 20, T16N, R101W (UW locality V-60008), 1789′ below Luman Tongue, Wasatch Formation, Sweetwater County, Wyoming.

Age.—Early early Eocene (Graybullian).

Referred specimens.—UW 15009, LM^1 or M^2; UW 15010, RM^3; UW 15262, RP^4; UW 15263, RM^1 or M^2.

Diagnosis.—Smallest species of the genus; upper molars relatively short with large conules and hypocone lingual to the protocone; hypoconulid on lower molars large and conical; posterolophid weakly developed on lower molars.

Etymology.—*ctenodactylops, Ctenodactylus*-like, in reference to features shared by this species with early Tertiary ctenodactyloids of Asia.

Description.—M_1 and M_2 of *Reithroparamys ctenodactylops* closely resemble those of other *Reithroparamys* with an entoconid isolated from the posterior cingulum with a partial hypolophid running buccally into the talonid basin. The trigonid of M_1–M_2 are narrower than the talonids with the protoconid and metaconid placed closely together. The trigonid basin is reduced to a narrow valley between the protoconid and metaconid which runs anteroposteriorly. The anterior cingulum on M^1–M^2 is a very short loph running from the buccal margin of the base of the metaconid buccally to the level of the apex of the protoconid. The mesoconid is relatively large and distinct. The hypoconulid is much enlarged, being nearly equal in size to the entoconid and hypoconid. Only a very low posteroloph connects the hypoconulid to the hypoconid. M_1 is smaller than M_2.

P^4 is submolariform and smaller than the upper molars. Both the protoloph and metaloph are fully developed with large dis-

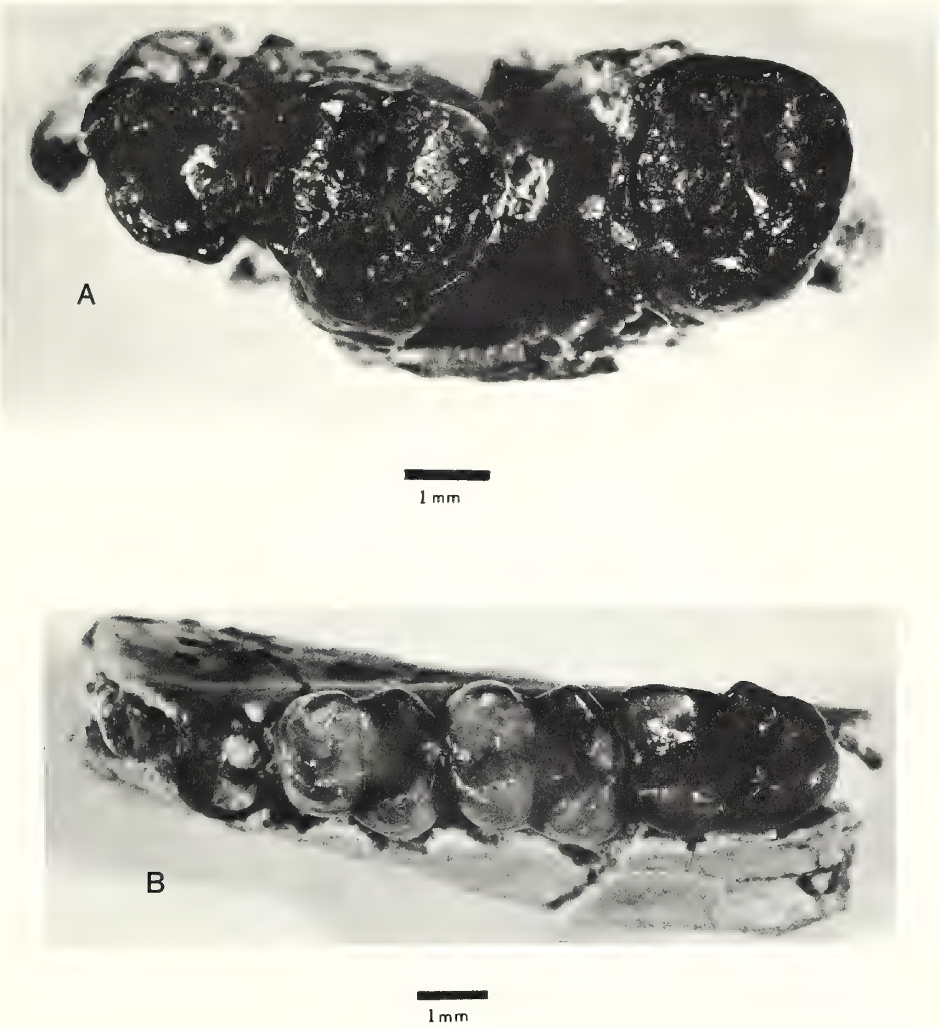


Fig. 11.—Cheek teeth of *Reithroparamys debequensis.* A) LdP^4–M^2, FMNH P 26151. B) LM$_1$–M$_3$, FMNH P 26726 (holotype).

tinct conules. The paracone and metacone are equal in height, the metacone is slightly more buccal than the paracone. The metaconule is larger than the protoconule. A minute mesostyle is present on the tooth. A distinct hypocone is posterior to the protocone. Both posterior and anterior cingulum run the entire width of the tooth.

The upper molar is relatively wider than is typical for reithroparamyines. The conules are relatively large. The protoloph and metaloph converge lingually at the protocone. A relatively large hypocone is present and positioned posterior and lingual to the protocone. The posterior cingulum runs buccally from the hypocone to the buccal margin of the tooth. The anterior cingulum originates at the buccal margin of the base of the protocone and runs to the buccal margin of the tooth. There is a minute mesostyle present on only one of the two known upper molars (UW 15009).

The protoloph and anterior cingulum of M^3 resemble those of the anterior upper molars. The tooth is expanded posterobuccally and reduced posterolingually, giving the tooth a nearly triangular occlusal outline. The metacone is absent, but the metaconule is quite large and part of the remaining metaloph which is a low, narrow loph that runs from the protocone to the posterobuccal margin of the tooth. There is a minute hypocone present, but it is more buccally placed than the protocone. The posterior cingulum runs the entire width as the tooth.

Discussion.—*Reithroparamys ctenodactylops* is clearly referable to this genus based on the presence of a partial hypolophid and isolation of the entoconid on the lower molars, relatively large hypocone on the upper molars, and submolariform P^4 with a distinct hypocone. It differs from other species of *Reithroparamys* in its smaller size, relatively shorter upper molars, larger conules and hypocone on the upper molars, hypocone being more lingually placed, and having the hypoconulid on the lower molars relatively larger and connected to the hypoconid only by a weak posterolophid. All of the features that distinguish *R. ctenodactylops* from other *Reithroparamys* are features present in early ctenodactyloids from Asia (Dawson et al., in press) and may represent the primitive dental morphology for rodents. Therefore, *R. ctenodactylops* represents the earliest and most primitive species of the genus.

Reithroparamys debequensis Wood, 1962

(Fig. 11)

Type specimen.—FMNH P 26726, left mandible with M_1–M_3.

Horizon and locality.—Type from Cherard Park, "about five miles southwest of Rifle, Colorado" (Wood, 1962:134), Lysite equivalent, Debeque Formation, Colorado. Referred specimens from the Knight Member, Wasatch Formation, Wyoming; and possibly Lysite equivalent, Willwood Formation, Wyoming.

Age.—Middle and late early Eocene (Lysitean and Lostcabinian).

Referred specimens.—USNM 22380 (from Knight Member, Wasatch Formation), FMNH P 26151 (from Debeque Formation) and possibly YPM 16525 (from Willwood Formation).

Discussion.—The lower molars of this species have been adequately described by Wood (1962). One specimen referred by Wood to *R. debequensis* (FMNH P 26503) from the same area as the holotype has been designated above as the type specimen of *Notoparamys arctios.* Wood (1962) also referred a maxilla with dP^4–M^2 from the Lysite equivalent of the Debeque Formation (FMNH P 26151) to *Paramys francesi.* Guthrie (1971) noted that this specimen was larger than any of the upper dentitions of *P. francesi* from the Wind River Basin and suggested that this specimen should be referred to *P. excavatus.* The molars of FMNH P 26151 differ from those of *P. excavatus* in being smaller and having the conules more lingually placed. The lingual portion of P^4 is present beneath dP^4 in FMNH P 26151. A distinct hypcone is present posterior to the protocone. All of the above features more nearly approach the condition in *Reithroparamys.* This specimen is referred here to *R. debequensis.*

An additional specimen (YPM 16525), here referred to *Reithroparamys* cf. *R. debequensis,* has been recovered from the Lysite level of the Willwood Formation in the Bighorn Basin. YPM 16525 consists of a nearly complete mandible with M_3. This specimen differs from the type of *R. debequensis* in being slightly larger and having the masseteric fossa terminate anteriorly below the posterior margin of M_1, farther forward than in *R. debequensis.* The masseteric crest and a strong chin process on YPM 16525 are very heavy and reminiscent of the mandible of *R. huerfanensis.*

Reithroparamys huerfanensis Wood, 1962

Type specimen.—AMNH 17031, left mandible with P_4–M_3 and some associated postcranial bones.

Horizon and locality.—Type locality X (see Robinson, 1966), Upper Huerfano Formation, Colorado. Referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Wyoming and Bridger Formation, Wyoming.

Referred specimens.—FMNH PM 21215 (from Cathedral Bluffs Tongue); UW 1328, FMNH PM 21047, FMNH PM 15155 (from Bridger Formation).

Discussion.—No additional specimens of *Reithroparamys huerfanensis* have been recovered since West's (1973) description of specimens from the Cathedral Bluffs and Bridger Formation. The very heavy knob on the side of the mandible of the holotype is not present on the referred material. Hence, the presence of this knob cannot be included in the diagnosis of this species (see Wood, 1962:136) because it is obviously an anomaly on the holotype.

Reithroparamys huerfanensis was described by Wood (1962) as having an angle of the mandible that was "considerably inflected" and most closely approached the hystricognathous condition. As discussed earlier, the condition in the mandible of *R. huerfanensis* is the result of a heavy chin process and the masseteric fossa bounded by a heavy ridge and not lateral displacement of the mandibular angle. Therefore, *R. huerfanensis,* like all other reithroparamyines, is not hystricognathous and not related to later South American rodents.

Acritoparamys, new genus

Type species.—*Acritoparamys francesi* (Wood, 1962).

Range.—Early to middle Eocene of Wyoming and Colorado.

Referred species.—*A. atwateri* (Loomis, 1907), *A. atavus* (Jepsen, 1937), *A. wyomingensis* (Wood, 1959*a*), and *A. pattersoni* (Wood, 1962).

Diagnosis.—Small rodents; posterior margin of the anterior root of the zygoma level with the center

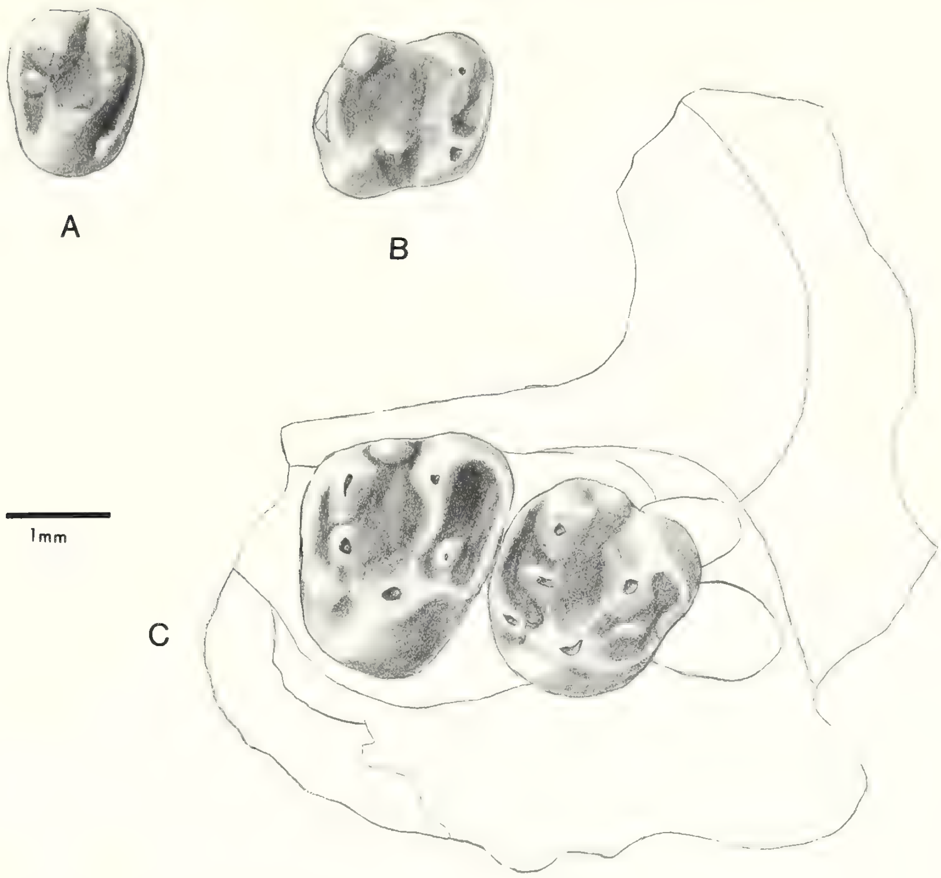


Fig. 12.—Cheek teeth of *Acritoparamys atavus* and *A. francesi.* A) *A. atavus,* LP^4, AMNH 22195. B) *A. atavus,* RM_2, PU 14220 (holotype). C) *A. francesi,* $RP^4–M^1$, CM 38727.

of P^4; masseteric fossa on the mandible terminates below center or anterior half of M_2; second minute mental foramen present on the mandible below the posterior root of P^4, posterior and ventral to the larger mental foramen; P^4 submolariform with protoconule and small hypocone; M^1 nearly square and equal in size to M^2; large buccolingually elongate hypoconulid present on lower cheek teeth, separated from the entoconid by a distinct groove and attached to the hypoconid by a low ridge; mesoconid small on lower molars; metaconid largest cusp on P_4 with reduced protoconid.

Etymology.—arctios, Greek, mixed or confused.

Comparisons.—Acritoparamys most closely resembles *Reithroparamys* among reithroparamyines, but differs from it by the lack of an entoconid crest that runs buccally into the talonid basin of the lower molars, having less well developed lophs on the cheek teeth, and having a less molariform P^4. *Acritoparamys* differs from *Microparamys, Lophiparamys,* and *Apatosciuravus* (described below) by having a relatively smaller hypocone on the upper molars, a more posterior position of the anterior root of the zygoma, and better developed hypoconulid and more isolated entoconid on the lower cheek teeth. *Acritoparamys* also lacks the separation of the anterior cingulum of the lower molars present in *Microparamys* and *Lophiparamys. Lophiparamys* also has minute crenulations on the basins of the cheek teeth not present in *Acritoparamys.*

Acritoparamys differs from all other ischyromyids by the features listed above in the diagnosis for the Reithroparamyinae.

Acritoparamys atavus (Jepsen, 1937)
(Figs. 12a, b)

Paramys atavus Jepsen, 1937.

Type specimen.—PU 14200, RM_2.

Horizon and locality.—Type and all referred specimens from Eagle Coal Mine, Bear Creek, Montana.

Age.—Latest Paleocene (Tiffanian).

Referred specimens.—AMNH 22195 (LP^4), and PU 14200c, AMNH 22155, AMNH 22156, AMNH 22163, AMNH 22166, AMNH 22199, CM 11552, CM 11690 (all incisors).

Emended diagnosis.—Smallest species of the genus; hyopconulid only weakly separated from entoconid on M_2; accessory loph runs buccally from the metaconid into the trigonid basin.

Discussion.—Only three additional incisors (CM 11552, CM 11690) can be added to the known record of this species. The two known cheek teeth of *Acritoparamys atavus* have been fully described elsewhere (Jepsen, 1937; McKenna, 1961; Wood, 1962). The presence of a hypocone and protoconule on P^4 and a distinct groove separating the posterolophid from the entoconid on M_2 distinguishes this species from *Paramys.* The enlarged hypoconulid on M_2 is known for *P. taurus,* but is also characteristic of *Acritoparamys.* Based on the morphology of the M_2 and P^4, *Paramys atavus* is more likely referable to *Acritoparamys.* It differs from all other species of this genus in its smaller size and narrower separation of the entoconid from the posterolophid of M_2.

Rose (1981) referred a number of specimens from the Clarkforkian of the Bighorn Basin to *P. atavus.* However, these specimens are smaller than any referred specimen of *A. atavus,* the trigonids of the lower molars are relatively narrower, and the posterolophid is continuous with the entoconid on the lower molars. The UMMP specimens referred by Rose (1981) to *Paramys atavus* are here identified as a new genus and species (see discussion below of *Apatosciuravus*), thus restricting the known range of *Acritoparamys atavus* to the Tiffanian Eagle Coal Mine.

Recently, Gingerich et al. (1980), Krause (1980) and Rose (1981) have referred the Bear Creek, Eagle Coal Mine fauna to the earliest Eocene Clarkforkian age. In its intial description by Simpson (1928, 1929*a*, 1929*b*), the Bear Creek fauna was recognized as late Tiffanian, an allocation followed by nearly all later workers. Rose (1981: Table 52) made a detailed faunal comparison of the Bear Creek fauna, and concluded it was Clarkforkian on the basis of the presence of two primates, a rodent, and a hyopsodont condylarth. Reexamination of the evidence shows the following. The rodent *Paramys atavus* (here referred to *Acritoparamys*) is unique to Bear Creek, its reported occurrence in the Clarkforkian of the Bighorn Basin is based on a misidentification by Rose (1981). The two primates, *Carpolestes nigridens* and *Plesiadapis dubius* are considered to be Clarkforkian species (Gingerich, 1976; Rose, 1975, 1981). The first primate, *C. nigridens,* is clearly present in both the Bear Creek locality and the Clarkforkian of the Bighorn Basin. However, this species may not be exclusively Clarkforkian because of referred material from Wasatchian localities (see Rose, 1981:62–63). The recognition of the other primate is quite tenuous. *Plesiadapis dubius* from Bear creek was originally identified as an indeterminate species of *Plesiadapis* (Simpson, 1928), based on a single isolated M_3. Gingerich (1976) referred this specimen to the Clarkforkian species *P. dubius* rather than the Tiffanian *P. fodinatus.* The only differences recognized by Gingerich between these two species were size, absence of a premolar, and morphology of the upper molars. The M_3 from Bear Creek (AMNH 22154) is well within the size range of *P. fodinatus* (Gingerich, 1976: Tables A-10, A-11) and larger than any specimens referred by Rose (1981: Table 12) to *P. dubius* from the Clarkforkian. The other features separating these two species of *Plesiadapis* cannot be applied to the known material from Bear Creek. Based on size, AMNH 22154 is closer to the Tiffanian *P. fodinatus* than the Clarkforkian species, but no specific identification can be made on such limited material.

Rose (1981) identified five specimens from Bear Creek as *Haplomylus* cf. *simpsoni* that were smaller than *H. simpsoni* from the Clarkforkian in the Bighorn Basin. Elsewhere, *Haplomylus* is only known from the earliest Eocene. If Bear Creek were Tiffanian, this would represent the earliest known specimens of this genus. Conversely, if Bear Creek were earliest Eocene, other animals in the fauna such as *Aphronorus,* would be the latest known representatives of otherwise Paleocene mammals.

Rose (1981: Table 52) compared the Bear Creek fauna with the fauna from a typical Clarkforkian locality (UMMP locality SC-188). He listed 43 species. Only seven of these are common to both localities. One is only identified to genus (*Dissacus*), one is misidentified from SC-188 (*Paramys atavus*), one is not clearly conspecific (*Haplomylus* cf. *simpsoni*), and three species are also known from the Tiffanian and/or Wasatchian outside the Bighorn Basin (*Phenacolemur pagei, Leipsanolestes siegfriedti, Phenacodus primaevus*). Only one species,

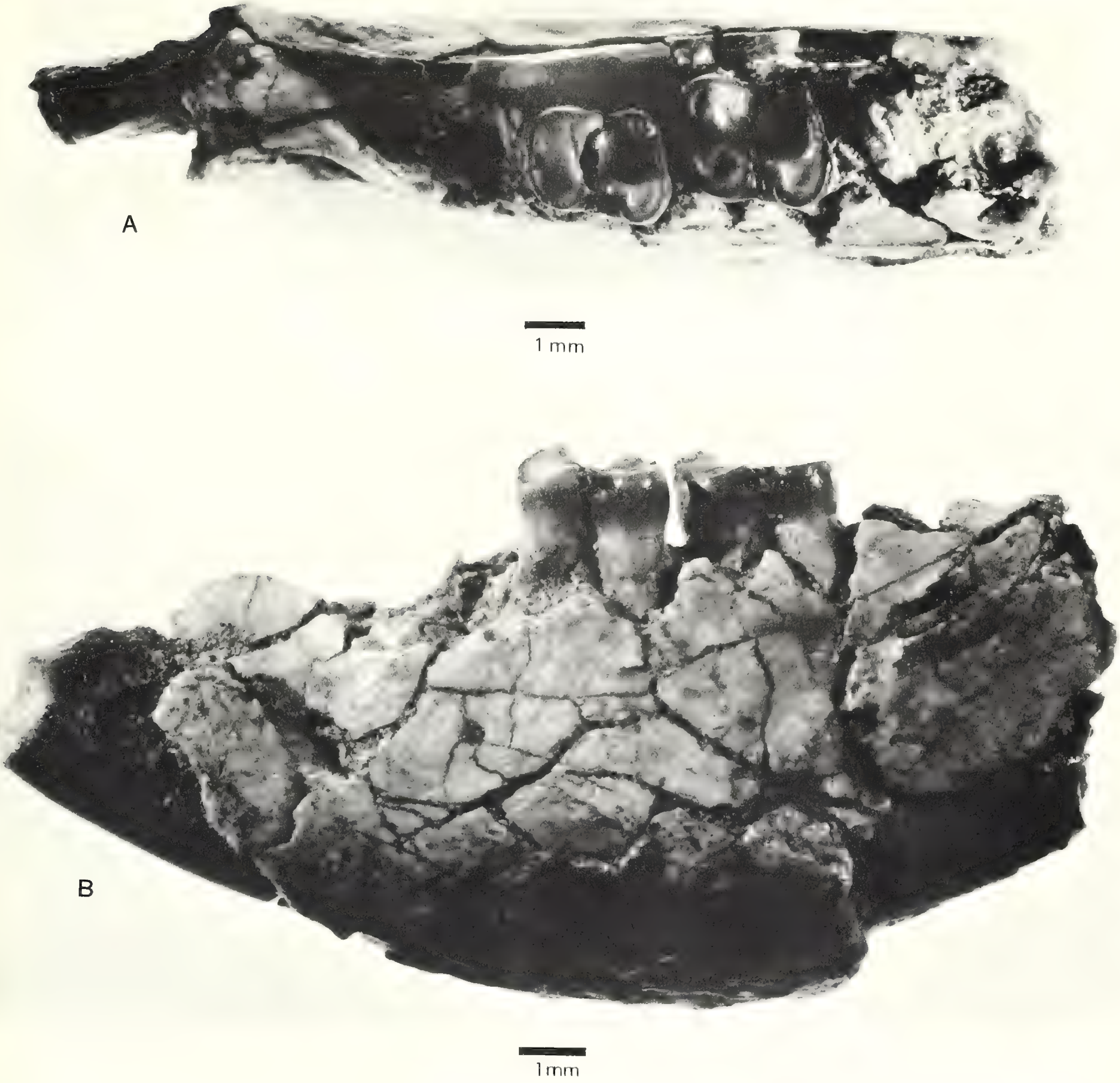


Fig. 13.—Holotype of *Acritoparamys atwateri,* ACM 180. A) Occlusal view of M_1–M_2. B) Lateral view of the mandible.

Carpolestes nigridens, is known only from both the Clarkforkian of the Bighorn Basin and Bear Creek. The possible occurrence of this species in the Wasatchian of the Bighorn Basin (Rose, 1981:62) and lack of it elsewhere outside the Bighorn Basin, may indicate that this species is regionally restricted rather than temporally restricted, as suggested by Rose (1975, 1981).

Overall, the Bear Creek fauna is more likely a unique late Tiffanian fauna as was originally suggested (Simpson, 1928, 1929*a,* 1929*b*; Jepsen, 1937) than a Clarkforkian one. The allocation of this fauna to a Clarkforkian age is questionable at best. The acceptance of a Tiffanian age for the Bear Creek fauna maintains *Acritoparamys atavus* as the earliest known rodent.

Acritoparamys atwateri (Loomis, 1907)
(Figs. 13, 14, Table 5)

Paramys atwateri Loomis, 1907.

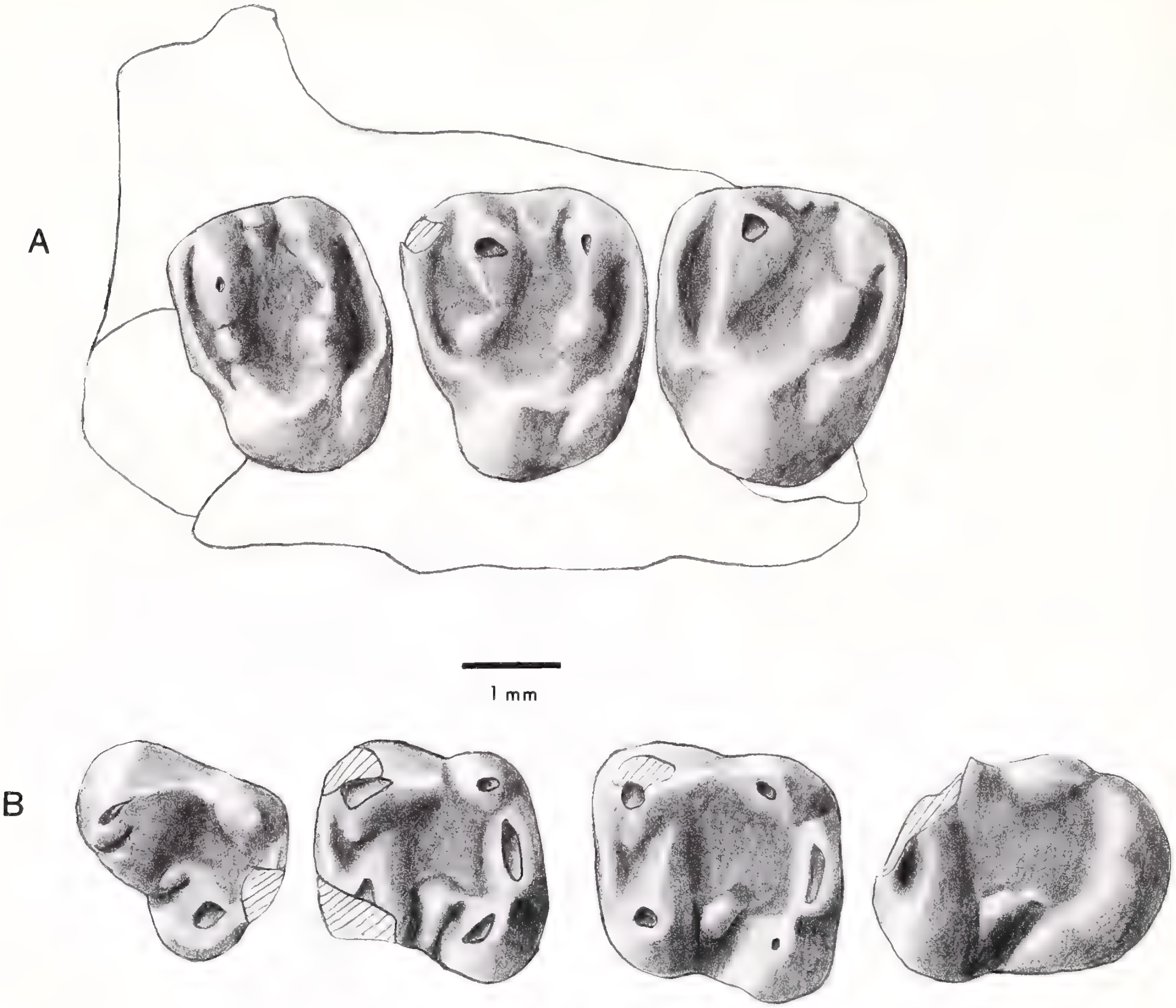


Fig. 14.—Cheek teeth of *Acritoparamys atwateri.* A) LP^4–M^2, AMNH 15710. B) LP$_4$–M$_3$, PU 18410.

Reithroparamys atwateri (Loomis) Wood, 1962.
Paramys annectens Rose, 1981.

Type specimen.—ACM 180, left mandible with M$_1$–M$_2$.

Horizon and locality.—Type from "foot of Tatman Mt." (Loomis, 1907:127), Willwood Formation, Wyoming. Referred specimens also from the Willwood Formation, and Wasatch Formation (Four Mile fauna), Colorado.

Age.—Earliest Eocene (Clarkforkian and Graybullian).

Referred specimens.—CM 12245, PU 18410, PU 19526, ROM 2180, UMMP 71177, AMNH 15710, USNM 19188, USNM 19189, and several unnumbered specimens from AMNH.

Emended diagnosis.—Small size; cusps on lower molars less bulbous than *A. francesi*; posterior arm of protoconid on molars extends lingually, nearly to the base of the metaconid; hypoconulid separated from entoconid by narrow valley.

Description.—The posterior margin of the anterior root of the zygoma is level with the center of P^4, just slightly more posterior than in *Acritoparamys francesi* (described below). P^4 is distinctly smaller than M^1 and shorter than that of *A. francesi.* The anterior cingulum is closely appressed to the protoloph. A minute mesostyle is present. The hypocone is larger than that of *A. francesi.* The protoconule is anterior to the paracone. The upper molars resemble those of *A. francesi* but do not have an enlarged metaconule or parastylar area on M^1 as in the latter.

The masseteric scar on the mandible extends anteriorly to below the middle of M$_2$. A doubled mental foramen is present as in all other species of the genus. The lower incisor is narrow transversely and flattened anteriorly. On the holotype (ACM 180) the anterior surface is slightly concave.

Table 5.—*Dental measurements of* Acritoparamys atwateri.

Specimen no.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
ACM 180	—	—	—	—	1.95	2.17	—	2.34	2.45	—	—	—
PU 19526 L*	—	—	—	—	—	—	2.30	2.25	2.40	3.10	2.25	2.4
PU 19526 R*	2.00	1.50	1.80	2.20	1.90	2.15	2.35	2.30	2.45	3.10	2.30	2.4
PU 18410	2.12	1.44	1.92	2.32	—	2.29	2.37	2.19	2.44	2.86	—	2.2
CU 12245	—	—	—	—	—	—	2.50	—	2.41	—	—	—
ROM 2180	2.06	1.47	1.87	2.34	1.92	2.18	2.49	2.23	2.40	—	—	—
UMMP 71177*	—	—	—	2.25	1.90	2.15	2.40	2.25	2.40	—	—	—
		P^4			M^1			M^2				
AMNH 15710	2.05	2.65	2.60	2.60	2.90	2.75	2.50	3.00	2.80			

* Measurements taken from Rose (1981).

The metaconid is much larger than the protoconid on P_4 but the difference in the sizes of these two cusps is not as great as in P_4 of *A. francesi.* P_4 is narrower anteriorly. The hypoconulid and posterolophid on the lower cheek of *A. atwateri* are distinct and separated from the entoconid. The mesoconid on the lower molars is a distinct cusp. The posterior arm of the protoconid extends lingually across the tooth, nearly closing off the trigonid basin posteriorly. The posterolophid forms a separate posterolingual lobe on M_3.

Discussion.—Acritoparamys atwateri differs from *A. atavus* in greater separation of the entoconid and posterolophid and relatively larger hypoconulid on M_2. P^4 of *A. atwateri* is nearly identical in pattern to that of *A. atavus,* but is substantially larger. *Acritoparamys atwateri* is nearly equal in size to *A. francesi* but differs in having less bulbous cusps, a smaller hypoconulid, longer posterior arm of the protoconid, and shorter P^4.

Loomis (1907) described *Paramys atwateri* based on a single mandible with heavily worn M_1–M_2 (ACM 180). Wood (1962) referred this species to *Reithroparamys* based on the separation of the entoconid from the posterolophid. Guthrie (1971) stated that the specimens referred to *R. atwateri* were just minor variants of *Paramys excavatus.*

The entoconid on M_1–M_2 of ACM 180 is isolated and the hypoconulid is a buccolingually elongate swelling on the posterolophid. These features separate ACM 180 from *P. excavatus* and are characteristic of reithroparamyines. The lack of an entoconid ridge on the molars and the presence of a second mental foramen on the mandible of *R. atwateri* make it referable to *Acritoparamys.*

Both Loomis (1907: Fig. 3) and Wood (1962: Fig. 45a) failed to figure or mention the major transverse crack in both molars of the holotype of *A. atwateri,* which has artificially elongated the teeth (see Fig. 13). Wood's (1962: Table 47) measurements of ACM 180 are not corrected for this elongation. The maxillae referred by Wood (1962) to *Paramys excavatus taurus* (AMNH 15710, USNM 19188, USNM 19189), as discussed previously, are more likely referred to *A. atwateri* (see discussion of *P. taurus*).

Wood (1962) included a mandible with P_4–M_2 from the Graybullian of the Bighorn Basin (ROM 2180) in the hypodigm of *Franimys amherstensis.* Rose (1981) questioned this location because the mandible was from a different level than the type of *F. amherstensis.* This specimen is clearly referable to *A. atwateri* based on size and morphology of the mandible and cheek teeth.

Rose (1981) described a new species, *Paramys annectens,* from the Clarkforkian of the Bighorn Basin, which was intermediate in size and morphology between *Paramys atavus* and *P. excavatus* (referring to *P. excavatus taurus*). However, Rose's specimens are equal in size and identical in morphology to Graybullian specimens of *A. atwateri* and should be referred to this species.

The shallow groove on I_1 of the holotype of *A. atwateri* (see Wood, 1962: Fig. 45b) is not present on any of the referred specimens. The variable occurrence of this feature is present in *Reithroparamys delicatissimus* and in species of *Thisbemys* and *Paramys.* Thus, it is not considered inconsistent for this character to be variable in *A. atwateri.*

One specimen from the Lysite level of the Bighorn Basin (AMNH 15139) and one from the Lysite Member of the Wind River Formation (AMNH 15610) were referred by Wood (1962) to *Paramys francesi* and *Reithroparamys atwateri* respectively. Both of thse specimens are identical to *A. atwateri* in morphology but are slightly larger (see Wood, 1962: Tables 22 and 47). These specimens are here referred to *Acritoparamys* cf. *A. atwateri.*

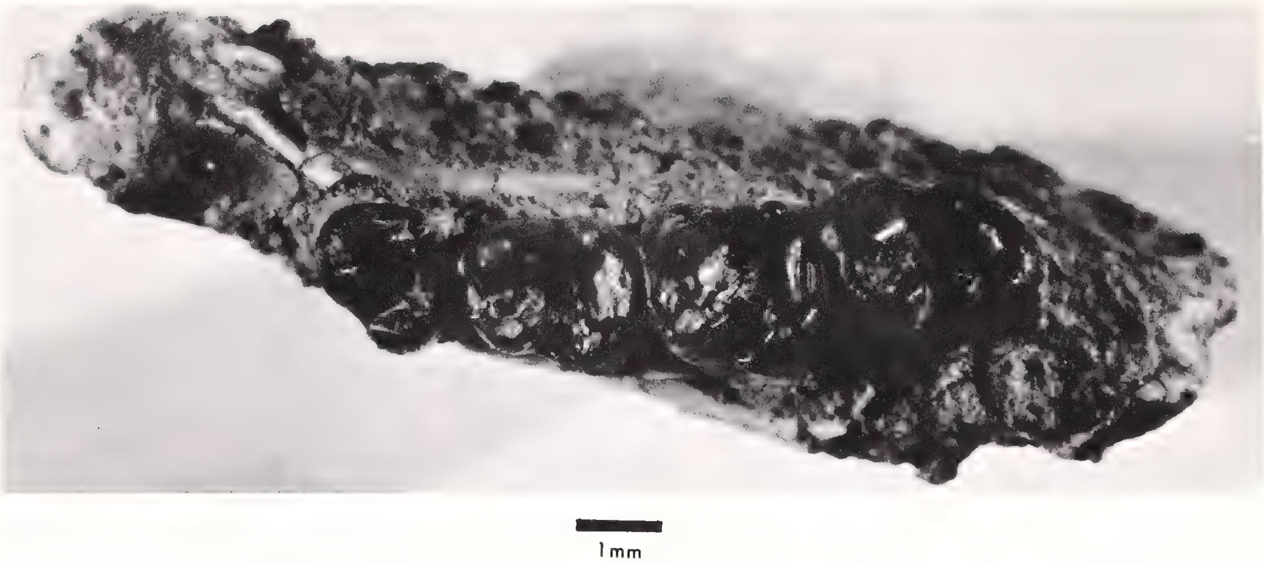


Fig. 15.—Lower dentition of *Acritoparamys francesi*, LP_4–M_3, CM 37170.

Acritoparamys francesi (Wood, 1962)
(Figs. 12, 15, Table 6)

Paramys francesi Wood, 1962.

Type specimen.—AMNH 14724, left mandible with P_4–M_3.

Horizon and locality.—Type from locality 1 (see Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wyoming. Referred specimens also from the Lost Cabin Member, and Knight Member, Wasatch Formation, Wyoming.

Age.—Late Early Eocene (Lostcabinian).

Referred specimens.—CM 21144, 21156, 21157, 21159, 21161, 21163–21166, 21169, 21171, 21933, 22221–22224, 22226–22233, 22249, 22536, 22842, 26511, 26512, 26519, 26521–26524, 26594, 27450, 27451, 29150–29152, 29158, 21965, 30957, 35839, 36509–36516, 36928, 37166, 37167, 37169, 37170, 37173, 37176, 38727–38735, and CU 42200, 42201, 44727, 44846, 44847 (from the Knight Member).

Emended diagnosis.—Small species; cusps on molars bulbous; P^4 nearly equal to M^1 in size; metaconule on P^4–M^2 enlarged, near size of metacone; posterior arm of protoconid on lower molars short, leaving trigonid basin widely open posteriorly; mesoconid minute to absent on lower molars.

Description.—The posterior margin of the anterior root of the zygoma is even with the middle of P^4. A prominent ridge originates buccal to P^3 and parallels the anterior margin of the zygoma, marking the insertion of the masseter muscle. The infraorbital foramen is small and unmodified.

P^3 is small and single rooted. P^4 is relatively large, approaching M^1 in size. The paracone is large and buccolingually elongate. The anterior cingulum is separated from the paracone and extends the entire width of the tooth. It is slightly expanded in the parastylar area making a slight anterior bulge. The protoconule is minute and slightly anterior to the paracone. A hypocone is present but minute. The metaconule is large, nearly equal to the metacone in size. A large mesostyle is present and closely appressed to the metacone and separated from the paracone by a deep valley.

The anterior cingulum on M^1 is expanded in the parastylar area, giving the tooth a convex bulge at the anterobuccal corner. As in P^4, the protoconule is small and positioned close to the protocone. The metaconule is slightly smaller than the metacone. A small mesostyle is present. M^2 is similar to M^1 but lacks the anterobuccal convexity and is slightly longer buccally than M^1. M^3 is unknown.

The masseteric fossa on the mandible ends anteriorly below the posterior margin of M_1 or anterior margin of M_2. A large mental foramen is present just anterior to P_4 only slightly below the alveolar margin. The diastema is shallow and short.

The lower incisor is flattened anteriorly, and the medial and lateral sides are parallel. Medially, the enamel extends about one-quarter of the dorsoventral height of the tooth, and laterally about half of the height.

P_4 is variable in shape. It varies in length from slightly less than 100% of the length of M_1 to about 50% of the length of M_1. A metaconid is large and makes up most of the trigonid. The protoconid is minute and situated low on the posterobuccal slope of the metaconid. The entoconid is isolated in most specimens but is entirely lacking on those specimens in which P_4 is markedly shortened. The posterolophid is made up of a distinct enlarged hypoconulid which is connected to the hypoconid by a low loph.

Mesoconids on M_1 and M_2 are reduced to low anteroposterior lophs connecting the protoconid and hypoconid on some specimens. The hypoconulid on the molars is even more pronounced than in P_4, and more distinctly separated from the entoconid. The trigonid basin of M_1–M_2 is minute, closed anteriorly, and

Table 6.—*Dental measurements of* Acritoparamys francesi *(in millimeters).*

Measurements	N	M	S	V	OR
P_4–M_3	5	9.66	.30	3.1	9.37–10.15
P_4 a–p	17	2.18	.14	6.6	1.81–2.43
tra	18	1.56	.12	7.5	1.37–1.72
trp	18	2.02	.14	7.0	1.82–2.30
M_1 a–p	42	2.34	.07	3.1	2.14–2.47
tra	36	1.94	.11	5.6	1.69–2.12
trp	40	2.20	.11	5.0	1.98–2.37
M_2 a–p	34	2.42	.09	3.7	2.27–2.66
tra	29	2.27	.10	4.5	2.10–2.47
trp	31	2.44	.12	4.7	2.23–2.65
M_3 a–p	11	2.55	.12	4.7	2.35–2.77
tra	9	2.26	.15	6.8	2.00–2.54
trp	9	2.15	.12	5.8	1.96–2.35
P^3 a–p	1	1.05	—	—	—
tra	1	1.09	—	—	—
P^4 a–p	7	2.20	.07	3.1	2.14–2.31
tra	7	2.44	.15	6.3	2.27–2.67
trp	7	2.53	.18	7.2	2.30–2.81
M^1 a–p	9	2.23	.06	2.8	2.13–2.33
tra	8	2.56	.09	3.5	2.41–2.69
trp	8	2.41	.08	3.5	2.28–2.51
M^2 a–p	6	2.30	.06	2.8	2.23–2.41
tra	6	2.52	.06	2.4	2.47–2.61
trp	6	2.34	.08	3.2	2.24–2.44

broadly open posteriorly. The posterior arm of the protoconid is short and low, completely disappearing with wear. M_3 is similar to M_1–M_2 but more elongate. The entoconid is reduced. The posterolophid forms an extra lingual lobe on the tooth.

Discussion.—*Acritoparamys francesi* differs from all other species of the genus in its more molariform P^4, more bulbous cusps, and wider separation of the posterolophid and entoconid on the lower molars.

Only three specimens of *A. francesi* are known from outside the type area of the Lost Cabin Member of the Wind River Formation. All three are from the Knight Member of the Wasatch Formation of southwestern Wyoming (USNM 19302, 22436, 22440), some of which have been previously referred to *Paramys excavatus* (Wood, 1962). These specimens do not differ from the topotypic material of *A. francesi* except in being slightly larger.

Guthrie (1971) suggested that *A. francesi* was ancestral to *Paramys wyomingensis* (here referred to *Acritoparamys*). This does not appear tenable at present because P^4 of *A. francesi* is already more advanced than in *A. wyomingensis* and the separation of the entoconid and posterolophid is not as wide in *A. wyomingensis.*

The Bridgerian *Paramys wyomingensis* is clearly referable to *Acritoparamys* based on the morphology of P^4 and the upper molars as described by Wood (1959*a*, 1962) and West (1969). The lower molars referred by West (1973) to *P. wyomingensis* have a distinct hypoconulid and a separation between the entoconid and posterolophid as in *Acritoparamys.* A maxilla with P^4–M^3 of *P. wyomingensis* (AMNH 97808) recovered from the same area as the holotype of the species has the posterior margin of the anterior root of the zygoma level with the middle of P^4, again, as in *Acritoparamys. Paramys wyomingensis* agrees with *Acritoparamys* in all features of the dentition. Hence, this species should be allocated to the latter genus as a distinct species.

Acritoparamys pattersoni (Wood, 1962)
(Fig. 16)

Reithroparamys pattersoni Wood, 1962

Type specimen.—FMNH P 26884, left mandible with P_4–M_1.

Horizon and locality.—Type and referred specimens from "southwest of Rifle, Colorado" (Wood, 1962:135), Lost Cabin equivalent, Debeque Formation, Colorado.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—FMNH P 26642, P. 26787, PM 258.

Discussion.—*Acritoparamys pattersoni* differs from all other species of the genus in its larger size, more molariform P_4, and doubled metaconule on the upper molars. The metaconid on P_4 of *A. pattersoni* is relatively smaller than in other species and the protoconid is nearly equal to it in height. The only known upper molar of *A. pattersoni* was figured by Wood (1962: Fig. 45j). It closely approaches *Reithroparamys delicatissimus* in having a multiple metaconule.

Guthrie (1971) considered *R. pattersoni* a junior synonym of *Paramys excavatus,* based on on the sample of *P. excavatus* from the Lost Cabin Member of the Wind River Formation. He stated that all specimens of *R. pattersoni* were just minor variants of *P. excavatus.* Clearly, the specimens referred by Wood (1962) to *R. pattersoni* from the Lost Cabin beds of the Wind River Basin are referable to *Paramys.* However, the type and topotypic material of *A. pattersoni* from the Debeque Formation are dis-

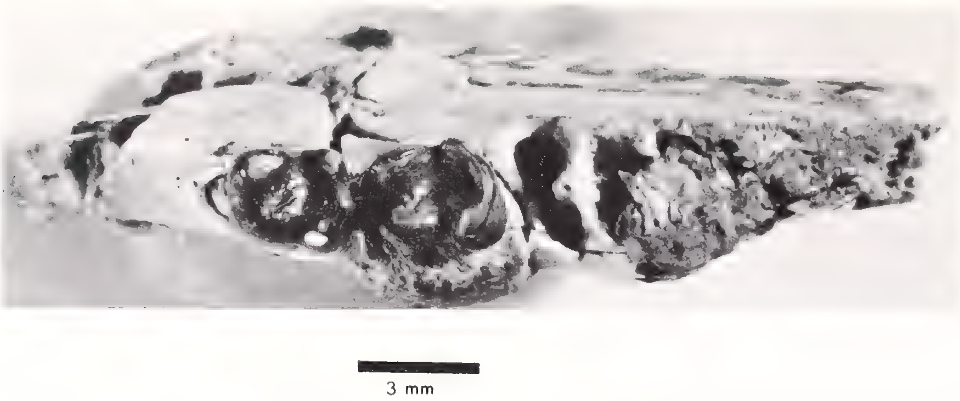


Fig. 16.—Holotype of *Acritoparamys pattersoni*, LP_4–M_1, FMNH P 26884.

tinct from *Paramys* and agree in molar and mandibular morphology with *Acritoparamys.*

Microparamys Wood, 1959*a*

Type species.—Microparamys minutus (Wilson, 1937).

Discussion.—Wood (1959*a*, 1962) diagnosed *Microparamys* as having a large infraorbital foramen. However, the infraorbital foramen in the only partial skull of *Microparamys* (described below) is not larger than is typical for early ischyromyids or sciuravids. The only feature that needs to be added to Wood's diagnosis is that the posterior margin of the anterior root of the zygoma is level with the anterior margin of P^4, farther forward than in any other ischyromyids, and similar to that in many sciuravids.

Wood (1959*a*) initially included two species from North America in *Microparamys, M. minutus* and *M. wyomingensis.* In his overall review of early ischyromyids, Wood (1962) recognized four additional species, *M. tricus* (Wilson, 1940) and three new species, *M. lysitensis, M. cathedralis,* and *M. wilsoni,* along with four indeterminate species (called sp. A, B, C, D). Dawson (1966) referred *Sciuravus dubius* (Wood, 1949) to *Microparamys,* and Wood (1974) named a new species from the early Oligocene of Texas, *M. perfossus.*

Dawson (1968*b*) questioned the inclusion of *M. wilsoni, M. lysitensis, M. cathedralis, M. wyomingensis,* and *Microparamys* sp. B in the genus. She identified the two specimens referred by Wood (1962) to *Microparamys* sp. C as *Sciuravus eucristadens.* West (1969), based on additional specimens, referred *M. wyomingensis* to *Paramys.* This species has been referred above to *Acritoparamys.* Guthrie (1971) referred both *M. lysitensis* and *M. cathedralis* to *Knightomys depressus,* and *Microparamys* sp. A to *Paramys.* Rose (1981) referred *Microparamys* sp. A to *Paramys atavus.*

The North American species of *Microparamys* accepted here are *M. minutus,* from the middle Eocene, *M. tricus, M. dubius,* and *Microparamys* sp. D, from the late Eocene, *M. perfossus,* from the early Oligocene, and two new species from the early Eocene, *M. reginensis* and *M. scopaiodon* (described below). The remainder of the North American species of *Microparamys* described earlier can be referred elsewhere, as follows: *M. lysitensis* and *M. cathedralis = Knightomys depressus*; *M. wyomingensis = Acritoparamys wyomingensis*; *Microparamys* sp. A = *Apatosciuravus bifax* (new genus and species); *Microparamys* sp. B = *Knightomys huerfanensis* (previously called *Paramys huerfanensis* by Wood, 1962); *Microparamys* sp. C = *Sciuravus eucristidens*; and *Microparamys wilsoni = Mysops.*

Microparamys reginensis, new species
(Fig. 17b, Table 8)

Type specimen.—CM 38762, right mandible with M_2–M_3.

Horizon and locality.—Type from CM locality Almagre # 2 (precise locality on file at CM), Almagre Member, San Jose Formation, Sandoral County, New Mexico. Referred specimen from CM locality Almagre #4 (same horizon as type).

Age.—Middle or late early Eocene (Lysitean or Lostcabinian).

Referred specimen.—CM 38763, LM_2–M_3.

Diagnosis.—Smallest species of the genus; M_2 square in occlusal outline; anterior cingulum separated from protoconid on M_2–M_3 by narrow valley

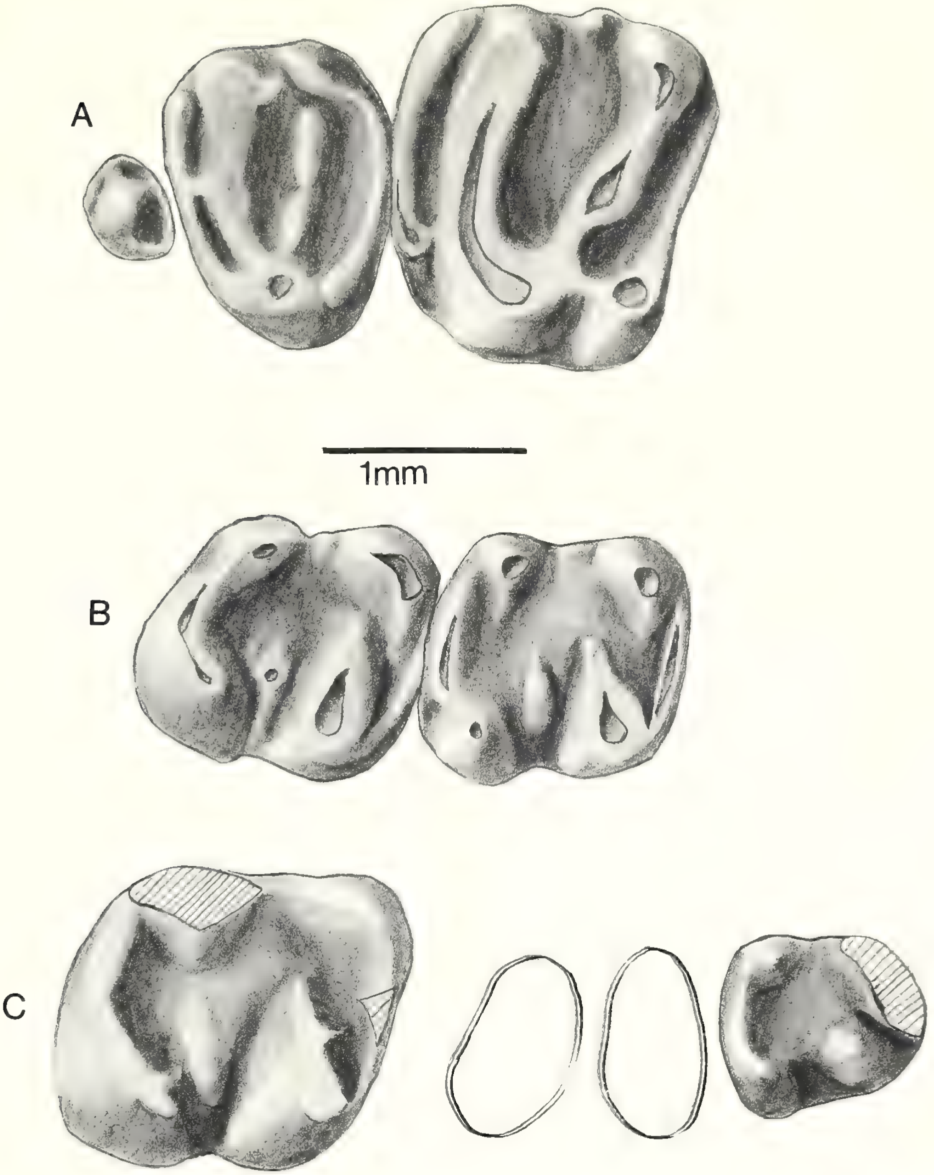


Fig. 17.—Holotypes of *Apatosciuravus* and *Microparamys.* A) *Apatosciuravus bifax,* LP^3–M^1, CM 38765. B) *Microparamys reginensis,* RM$_2$–M$_3$, CM 38762. *M. scopaiodon,* RP$_4$, M$_2$, CM 36196.

which disappears with wear; mesoconid small and anteroposteriorly compressed; minute metastylid on lower molars.

Etymology.—Specific name for Regina, New Mexico, near where the type was recovered.

Description.—*Microparamys reginensis* is the smallest North American species of this genus described. The mandible is slender and the masseteric fossa extends anteriorly to below the posterior root of M$_1$. Two mental foramina are present. The larger anterior foramen is situated high on the mandible below the anterior margin of P$_4$. The second minute foramen is placed more ventrally on the mandible than the first and is below the anterior root of P$_4$.

From the alveoli, it is apparent that P$_4$ is smaller than M$_1$. M$_2$ appears to be larger than M$_1$. The anterior cingulum on M$_2$–M$_3$ is separated from the protoconid by a minute valley which disappears with wear. The posterior arm of the protoconid runs directly lingually across the tooth nearly closing off the trigonid basin posteriorly. A small isolated mesoconid is present and is slightly anteroposteriorly compressed, extending lingually into the talonid basin. The posterior cingulum connects to the entoconid on M$_2$. A minute metastylid is present on the posterolingual slope of the metaconid. This cuspule is eliminated on the referred specimen due to heavy wear.

The lower incisor is narrow, parallel sided and convex anteriorly. Enamel extends about one-third the dorsoventral height of the incisor on the lateral surface, and only very slightly onto the medial surface.

Discussion.—*Microparamys reginensis* is smaller than any other species of the genus. The anterior cingulum does not terminate buccally as a small cuspule as in *M. minutus* and other later species. The lingual extension of the mesoconid on the lower molars of *M. reginensis* is present only on one other species of *Microparamys* (described below as new species). The M_2 and especially M_3 of *M. reginensis* are more nearly rectangular in occlusal outline, as opposed to rhomboidal, than in other species of *Microparamys.*

Microparamys scopaiodon, new species
(Fig. 17c, Table 8)

Type specimen.—CM 36196, right mandible with P_4 and M_2 with associated upper molar.

Horizon and locality.—Hackberry Hollow, Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Diagnosis.—Near size of *M. minutus*; P_4 markedly smaller than molars; occlusal pattern of P_4 simple, cusps reduced to isolated cuspules; anterior cingulum short and separated from protoconid on M_2; molars moderately lophate; posterolophid separated from entoconid by narrow groove; posterior arm of protoconid parallel to anterior cingulum to the base of the metaconid; no ectolophid present on M_2; mesoconid anteroposteriorly compressed.

Etymology.—*scopaios,* Greek, dwarf; *odon,* Greek, tooth.

Description.—A single upper molar (M^1 or M^2) of *Microparamys scopaiodon* is preserved in the holotype. Because the specimen has been exploded by a concretion, this tooth cannot be prepared without destroying it entirely. The only observable feature of the upper molar is that there is no distinguishable protoconule on the protoloph. The length of the tooth can be measured (a–p = 1.32 mm).

The masseteric fossa on the mandible ends anteriorly below the posterior end of M_1 or anterior end of M_2. A single mental foramen may be present below the anterior extent of P_4. This area is badly damaged in the holotype, so the presence of any accessory foramina cannot be determined.

P_4 is very small and single rooted. It is more reduced relative to the molars than in any other species of *Microparamys.* All of the major cusps on P_4 (metaconid, protoconid, entoconid, hypoconid) have been reduced to small isolated marginally placed cuspules. The top of the metaconid is broken away, but from the size of the base of this cusp, it is the largest on P_4. It is placed just slightly anterior to the protoconid, and is separated from the latter by a narrow but relatively deep valley. There is no trace of a mesoconid or ectolophid. The posterior cingulum is the only recognizable loph on P_4. It is separated from the entoconid by a groove. The anterior width is narrower than the posterior width.

Only the alveolus for M_1 is preserved in CM 36196. M_1 is distinctly larger than P_4 but smaller than M_2. The anterior cingulum on M_2 is relatively short, arising from the metaconid and running buccally even with the apex of the protoconid. The posterior arm of the protoconid is a pronounced loph running approximately parallel with the anterior cingulum, ending lingually at the base of the metaconid. The anterior cingulum is separated from the posterior arm of the protoconid by a deep valley. The mesoconid is also quite distinct and anteroposteriorly compressed, extending into the talonid basin. The posterolophid originates from the hypoconid and is separated from the entoconid by a distinct groove. A relatively broad hypoconulid is present on the posterolophid. Only the roots of M_3 are preserved in the holotype. It appears that M_3 is longer but narrower than M_2.

The lower incisor is narrow, convex anteriorly, and gently convex on its lateral surface. Enamel extends posteriorly about one quarter of the dorsoventral height of the tooth on the medial side and approximately half of the height on the lateral side.

Discussion.—*Microparamys scopaiodon,* though clearly referable to *Microparamys,* shows great similarity of the middle Eocene genus of sciuravid *Pauromys* Troxell (1923). The height of the lophs on the molars, reduction in size of P_4, anteroposterior compression of the mesoconid on M_2, entoconid separated from the posterolophid, and protoconid isolated with a long posterior arm that runs to the base of the metaconid paralleling the anterior cingulum on *M. scopaiodon* are similarities with *Pauromys* (see Dawson, 1968*b*; Wood, 1959*b*).

The features that separate *M. scopaiodon* from *Pauromys* appear to be just primitive ischyromyid features. The anterior cingulum of M_2 of *M. scopaiodon* is widely separated from the protoconid, as in *Pauromys* and *Microparamys,* but does not extend as far buccally as it does in either of these genera. The anterior cingulum arises from the metaconid in *M. scopaiodon,* as is typical for *Microparamys,* unlike that of *Pauromys* in which the anterior cingulum runs to the lingual margin of the tooth anterior to the metaconid. *Microparamys scopaiodon* also lacks the hypolophid that runs buccally from the entoconid in *Pauromys* and connects to the center of the posterolophid. The masseteric fossa on the mandible of *M. scopaiodon* does not extend as far forward as in *Pauromys,* resembling *Microparamys* in this feature. In *Pauromys,* a minor loph extends buccally from the metaconid into the valley that separates the anterior cingulum and posterior arm of the protoconid. This feature is not present in *M. scopaiodon.*

P_4 of *M. scopaiodon* is clearly reduced in size and is greatly simplified, having all of the major cusps reduced to small isolated cuspules with no connecting lophs. This relative reduction of the cusps of P_4 is not present in *Pauromys*. P_4 of *M. scopaiodon* has a large single root, whereas in *Pauromys*, P_4 is double rooted.

Microparamys sp. (Debeque)
(Fig. 18a, Table 7)

Referred specimen.—FMNH 624-39, partial skull with RM^1.

Horizon and locality.—Southwest of Rifle, Colorado, Lysite equivalent, Debeque Formation, Colorado.

Age.—Middle early Eocene (Lysitean).

Description.—The position of the anterior root of the zygoma is far anterior of the tooth row, its posterior extent is level with P^3. The ridge marking the attachment of the masseter to the zygoma originates anterobuccal to P^3 and parallels the anterior margin of the zygoma. A small bony swelling is present on the rostrum ventral to the infraorbital foramen. The infraorbital foramen is small and unmodified. The incisive foramina are relatively long and narrow. The premaxillary-maxillary suture is positioned laterally on the palate at the anterior end of the infraorbital foramen, runs medially across the palate with many minute crenulations, then runs directly anterior to the posterolateral margin of the incisive foramen.

The rostrum appears to be relatively deep but narrow, although lateral compression of the skull may have altered the proportions of the skull. Anterior to the base of the zygoma is a broad valley running obliquely across the lateral margin of the rostrum, bounded posteriorly by the masseter scar on the zygoma and anteriorly by a low ridge which runs parallel to the masseter scar of the zygoma, possibly for the attachment of the *masseter superficialis* muscle.

Discussion.—Due to the fragmentary nature of FMNH 624-39, very little can be determined about the skull of *Microparamys* except that it follows the general pattern of early ischyromyid skulls. The infraorbital foramen is proportionally the same size as in other reithroparamyines. The rostrum is relatively shorter than in paramyines, similar to that of *Reithroparamys*.

The unique groove on the lateral side of the palate anterior to the tooth row in FMNH 624-39 is also present on the holotype of *Apatosciuravus bifax* (described below). The small swelling ventral to the infraorbital foramen which marks the anterior wall of the groove is similar to the knob for the attachment of the *masseter superficialis* in sciuromorphous rodents (see Wood, 1974; Korth, 1980).

There is no modification of the ventral side of the zygoma or infraorbital foramen on FMNH 624-39 which would indicate modification of the masseter.

The apparent anterior movement of the zygoma in *Microparamys* may be related to the anterior attachment of the *masseter superficialis*. However, in sciuravids there is no swelling below the infraorbital foramen but the zygoma is at least as far anterior as in *Microparamys*.

Table 7.—*Measurements of upper teeth of* Microparamys *sp. (Debeque) and* Apatosciuravus bifax *(in millimeters).*

Measurements		*Apatosciuravus bifax*			*Microparamys* sp.
		CM 38765			
		L	R	TTM 7992	FMNH 624-39
P^3	a–p	0.38			
	tra	0.56			
P^4	a–p	1.09	1.12	1.22	
	tra	1.41	1.40	1.55	
M^1	a–p	1.52	1.48	1.43	1.44
	tra	1.71	1.70	1.55	1.44
	trp	1.66	1.62	1.60	1.42
M^2	a–p			1.40	
	tra			1.63	
	trp			1.49	
M^3	a–p			1.47	
	tra			1.50	
I^1	a–p	—		2.23	
	tra	1.39		1.16	

FMNH 624039 is equivalent in size to the lower jaws identified as *M. reginensis*. It is impossible to prove that these two mandibles are the same species as FMNH 624-39. Recovery of more material from the Debeque and San Jose Formations is needed before association can be made.

Microparamys sp. (Lost Cabin)
(Fig. 18b, Table 8)

Referred specimens.—CU 44712, CU 44725 (isolated lower molars).

Horizon and locality.—Deadman Butte locality (see Stucky and Krishtalka, 1982), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Discussion.—Two isolated lower molars from the Lost Cabin Member are quite similar in morphology to the Bridgerian *Microparamys minutus*. The major difference between the Lost Cabin specimens of *Microparamys* and *M. minutus* is in the larger size of the Lost Cabin species. There is no buccal cuspule on the anterior cingulum of the Lost Cabin specimens as in later species of *Microparamys*.

Lophiparamys Wood, 1962

Type species.—*Lophiparamys murinus* (Matthew, 1918).

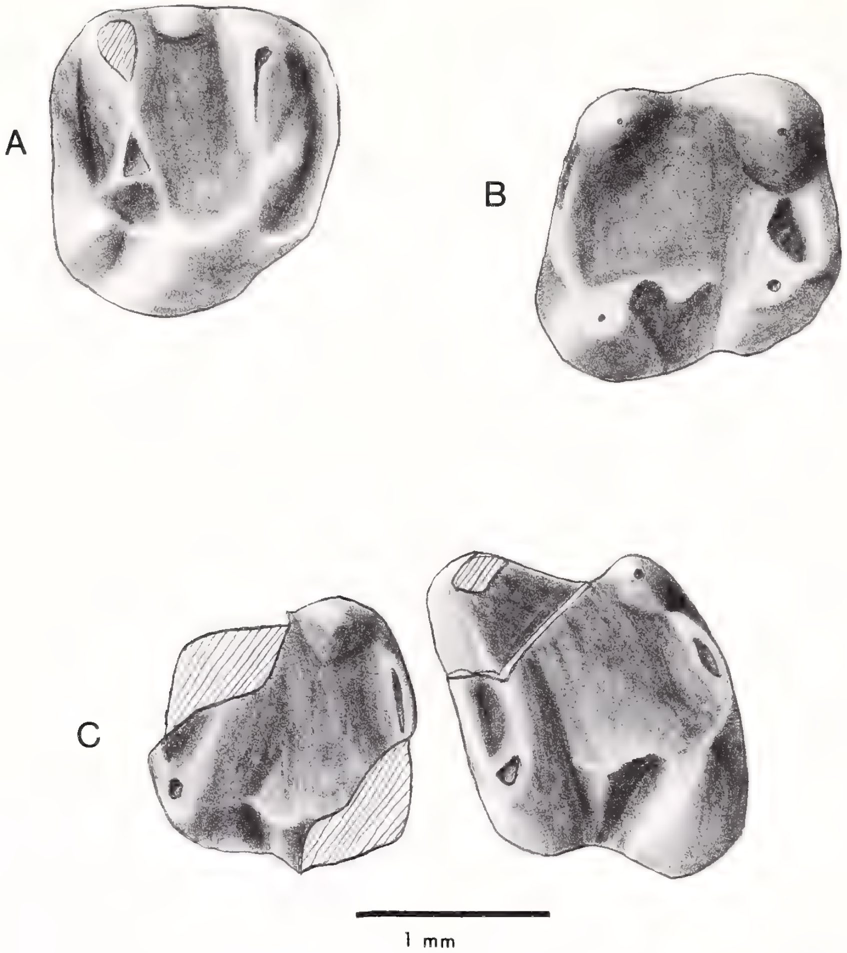


Fig. 18.—Molars of *Microparamys* sp. and an indeterminate reithroparamyine. A) *Microparamys* sp. (Debeque), RM^1, FMNH 624-39. B) *Microparamys* sp. (Lost Cabin), RM$_1$ or M$_2$, CU 44712. C) indeterminate reithroparamyine, LM$_1$–M$_2$, AMNH 17005.

Lophiparamys murinus (Matthew, 1918)

Paramys murinus Matthew, 1918.
Lophiparamys murinus (Matthew) Wood, 1962.

Type specimen.—AMNH 15131, associated mandibles with LP$_4$–M$_3$ and RM$_1$–M$_3$.

Horizon and locality.—Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Discussion.—The holotype (AMNH 15131) remains the only known specimen of *Lophiparamys murinus.* This specimen has been adequately figured and described elsewhere (Matthew, 1918; Wood, 1962). Nothing has been added to our knowledge of this species since its original description (Matthew, 1918) and subsequent discussion (Wood, 1962).

Lophiparamys debequensis Wood, 1962

Type specimen.—FMNH PM 1217, LM$_1$.

Horizon and locality.—Type from "confluence of Shooty and Scenery Gulches, seven miles east-northeast of the junction of White River and Piceance Creek, Rio Blanco County" (Wood, 1962:169), Lysite equivalent, Debeque Formation Colorado. Referred specimens from the Lysite Member, Wind River Formation, Wyoming and Almagre Member, San Jose Formation, New Mexico.

Age.—Middle and possibly late early Eocene (Lysitean and possibly Lostcabinian).

Referred specimens.—FMNH PM 1213 (from Debeque Formation); AMNH 48169 (from San Jose Formation); and CM 38709, ACM 2540, ACM 2575 (from Lysite Member).

Discussion.—Previously, *Lophiparamys debe-*

Table 8.—*Measurements of lower teeth of some reithroparamyines (in millimeters).*

	P_4			M_1			M_2			M_3		
Measurements	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
Apatosciuravus bifax												
PU 18419	1.31	0.86	1.07	1.41	—	—	—	—	—	—	—	—
CM 36643	—	—	—	1.48	1.24	1.49	—	—	—	—	—	—
ACM 10997	—	—	—	—	—	—	1.58	1.55	1.78	—	—	—
WAM 175	—	—	—	1.33	1.11	1.21	—	—	—	—	—	—
UMMP 65244*	1.10	0.85	1.00	—	1.30	—	1.70	1.30	—	1.70	—	—
UMMP 69871*	1.30	0.85	1.20	1.60	1.30	1.60	1.70	1.50	1.70	—	—	—
UMMP 71173*	—	—	—	—	—	1.50	1.65	1.45	1.70	—	—	—
Microparamys scopaiodon												
CM 36196	0.99	0.61	0.79	—	—	—	1.55	1.36	1.40	—	—	—
Microparamys reginensis												
CM 38762	—	—	—	—	—	—	1.19	1.16	1.21	1.30	1.25	1
CM 38763	—	—	—	—	—	—	1.29	—	1.20	1.29	1.18	—
Microparamys sp. (Lost Cabin)												
CU 44712	—	—	—	1.46	1.32	1.50	—	—	—	—	—	—
CU 44725	—	—	—	1.48	1.42	1.53	—	—	—	—	—	—
reithroparamyine indeterminate												
AMNH 17005	—	—	—	—	—	—	1.41	1.47	1.56	—	—	—

* Taken from Rose (1981).

quensis has been reported from the Lysite equivalent of the Debeque Formation (Wood, 1962), Lysite Member of the Wind River Formation (Wood, 1965; Guthrie, 1967), and the Lost Cabin Member of the Wind River Formation (Guthrie, 1971). A mandible with M_2–M_3 (CM 38709) has since been collected from the Lysite Member, Wind River Formation along with a partial mandible with M_3 from the San Jose Formation (AMNH 48169).

The occurrence of *L. debequensis* in the Lost Cabin fauna is questionable. Guthrie (1971:73) cited only two specimens of cheek teeth of *L. debequensis* (CM 22234, CM 22235) from the Lost Cabin fauna by number and figured both of them (Guthrie, 1971: Figs. 14a, 14b). In his tables of measurements, he (1971: Table 19) listed three cheek teeth, a P_4 and two M_3s. According to the measurements given by Guthrie, CM 22235 and the two M_3s are comparable in size to other specimens of *L. debequensis* (see Wood, 1962: Table 57; Wood, 1965: Table 1). However, measurements taken from Guthrie's figures are slightly larger than the measurements given for *L. woodi* (Guthrie, 1971: Table 19), the largest species of the genus.

The two specimens cited and figured by Guthrie, CM 22234 and CM 22235, cannot be found in the Carnegie Museum of Natural History collection. In fact, there is no record in the systematic files at Carnegie Museum of Natural History that these specimens were ever catalogued. Hence, until the specimens cited by Guthrie can be found and their measurements can be matched with either the tables or figures, *L. debequensis* should not be considered as a part of the Lost Cabin fauna.

Lophiparamys woodi Guthrie, 1971

Type specimen.—CM 22241, LM_3.

Horizon and locality.—Type and referred specimens from locality 4 (Guthrie, 1971), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—CM 22236–22240 (all isolated teeth).

Discussion.—No new material of *Lopiparamys woodi* has been recovered since its original description (Guthrie, 1971). This species differs from *L. murinus* and *L. debequensis* in being larger and having a more finely crenulate enamel surface on the cheek teeth.

Reithoparamyine genus and species indeterminate

(Fig. 18c, Table 8)

Referred specimen.—AMNH 17005, left mandible with M_2 and partial M_1.

Horizon and locality.—Elk Creek, Willwood Formation, Wyoming.

Age.—Early early Eocene (Graybullian).

Description.—AMNH 17005 is a small rodent (Table 8). The masseteric fossa on the mandible terminates anteriorly below the anterior root of M_2. No other features of the mandible can be determined.

M_2 is anteroposteriorly compressed, giving the tooth a transversely elongate appearance. The trigonid is nearly equal in width to the talonid. The trigonid basin of M_1 and M_2 is minute and closed anteriorly and posteriorly. A large, transversely elongate hypoconulid is present on both M_1 and M_2, and the entoconid is isolated from the hypoconulid. The ectoloph is weak.

Discussion.—The anterior position of the masseteric fossa on the mandible, isolated entoconid and enlarged hypoconulid on M_1–M_2 make AMNH 17005 clearly referable to the Reithroparamyinae. The unique feature of AMNH 17005 is the anteroposterior compression of M_2. Only one other ischyromyid has similar proportions of M_2, *Uriscus californicus* Wood (1962) from the late Eocene of California. This does not imply any close relationship between AMNH 17005 and *Uriscus. Uriscus* lacks the enlarged hypoconulid of reithroparamyines and the masseteric fossa does not extend as far anteriorly on the mandible.

The occurrence of AMNH 17005 in the Graybullian shows the greater diversity of small *Microparamys*-sized rodents in the early Eocene than was previously known.

Subfamily ?Reithroparamyinae

Apatosciuravus, new genus

Type species.—*Apatosciuravus bifax,* new species.

Range.—Earliest Eocene of Wyoming and Colorado.

Referred species.—Type species only.

Diagnosis.—Small rodents; posterior margin of anterior root of zygoma level with P^3; double mental foramen on the mandible; P_4^4 small relative to molars with distinct hypocone; metaloph and metacone poorly developed on P^4; upper molars cuspate with weak loph development and relatively large hypocones; trigonids of lower molars much narrower than talonids; anterior cingulum continuous with protoconid; small but distinct hypoconulid present on lower cheek teeth.

Etymology.—*apate,* Latin, false; *Sciuravus,* possibly related rodent.

Comparisons.—*Apatosciuravus* differs from *Reithroparamys* and *Acritoparamys* in the more anterior position of the anterior root of the zygoma, less molariform P^4, larger hypocone on M^1–M^2, and less well developed hypoconulid on P_4–M_2. *Apatosciuravus* differs from *Microparamys* and *Lophiparamys* in having a larger hypocone on M^1–M^2 and lacking an anterior cingulum on the lower molars separate from the protoconid. No other reithroparamyine has the buccolingual compression of the trigonids of M_1–M_2 that is present in *Apatosciuravus. Apatosciuravus* differs from paramyines, ailuravines and pseudoparamyines by the same features as all other reithroparamyines.

Apatosciuravus bifax, new species

(Fig. 17a, Tables 7, 8)

Microparamys sp. A Wood, 1962.

Type specimen.—CM 38765, partial palate and rostrum with RP^4–M^1 and LP^3–M^1.

Horizon and locality.—Type from Dorsey Creek, Willwood Formation, Wyoming. Referred specimens also from the Willwood Formation and East Alheit Pocket Quarry, Four Mile Fauna, Wasatch Formation, Colorado.

Age.—Earliest Eocene (Clarkforkian to Graybullian).

Diagnosis.—As for genus.

Referred specimens.—TTM 7992, PU 18419, WAM 175, CM 36643 (from Gray Bull beds, Willwood Formation); UMMP 65244, 69219, 29871, 71173, ACM 10997 (from Clarkforkian Willwood Formation); six unnumbered specimens from AMNH (from Four Mile fauna).

Etymology.—*bifax,* Latin, two-faced.

Description.—The position of the anterior root of the zygoma, size of the infraorbital foramen, and presence of a bony knob anterior to the tooth row are identical to that described above for *Microparamys.*

P^3 is minute and single rooted. It has a major central cusp with two very low ridges running posteriorly from it. The lingual ridge runs posteriorly from the lingual edge of the main cusp and curves buccally, defining a small shallow posterolingual basin. The second loph originates from the center of the main cusp and runs posterobuccally.

P^4 is small relative to M^1. The tooth is dominated by four low lophs (anterior cingulum, protoloph, metaloph, posterior cingulum). Both cingula run the entire width of the tooth. The metacone is reduced to a small cuspule at the posterobuccal corner of the tooth. The conules are reduced to minor swellings on the protoloph and metaloph, and cannot be distinguished from the continuous lophs after moderate wear. A small but distinct hypocone is present. The mesostyle is minute.

The molars are also dominated by four low, but continuous transverse lophs. The protoconule is not recognizable on the protoloph of any of the available specimens. A minute metaconule is distinguishable on the metaloph until late stages of wear. The anterior cingulum terminates buccally as a minute cuspule anterior to the protocone. The protoloph and metaloph on M^1–M^2 converge toward the cresentic protocone. A distinct mesostyle is present on the molars.

The anterior cingulum and protoloph of M^3 are similar to those of M^1 and M^2. The metacone is posteriorly and lingually placed, giving the tooth a triangular occlusal outline. The metacone appears to be reduced in size, and the posterior cingulum shortened, but this is difficult to determine because the only known M^3 of *A. bifax* (TTM 7992) is heavily worn in the area.

The upper incisor is long anteroposteriorly and narrow. The anterior surface is slightly convex and the medial and lateral sides are parallel. Enamel extends only slightly onto the lateral side, and does not extend onto the medial side.

The masseteric fossa on the mandible terminates anteriorly below the middle or posterior half of M_2. Mental foramina are preserved on only one specimen (PU 18419). A relatively small mental foramen is present high on the side of the mandible just anterior and ventral to the anterior margin of P_4. A second minute foramen is directly posterior to the first, just posterior to the center of P_4.

Both Wood (1962; as *Microparamys* sp. A) and Rose (1981; as *Paramys atavus*) have adequately described the lower cheed teeth of *A. bifax*. The unique features of the lower cheed teeth are the small P_4, and narrow trigonids of the molars.

Discussion.—*Apatosciuravus bifax* differs from *Microparamys* in not having the anterior cingulum completely separated from the protoconid on the lower molars, having a larger hypocone on the upper molars, lacking a metastylid and having a narrower trigonid on the lower molars. In size, *A. bifax* is approximately equal to the early Oligocene *Microparamys perfossus* Wood (1974).

Apatosciuravus bifax shares many features with both *Microparamys* and sciuravids: 1) anterior position of the zygoma and masseteric fossa on the mandible; 2) hypocone on P^4; and 3) large hypocone on the upper molars. *Apatosciuravus bifax* also has the attachment for what is believed to be the *masseter superficialis* present on the skull of *Microparamys*. The trigonid basin of *A. bifax* is similar to that of the indeterminate reithroparamyine described above.

Wood (1962) originally identified *Microparamys* sp. A from the early Wasatachian (later considered Clarkforkian by Rose, 1981) of the Bighorn Basin based on an isolated molar (ACM 10997), and a partial mandible with a heavily worn M_1 (WAM 175), but noted that there was a difference in the size of the two specimens. Guthrie (1971) referred Wood's *Microparamys* sp. A to *Paramys*, and along with a number of other synonymies, he concluded that the earliest North American species of *Microparamys* did not occur until the Bridgerian.

Rose (1981) referred the isolated molar of *Microparamys* sp. A (ACM 10997) to *Paramys atavus*, along with several more specimens from the Bighorn Basin. As discussed above, all of the material referred by Rose (1981) to *Paramys atavus* except for those from Eagle Coal Mine is here allocated to *A. bifax*. The holotype of *A. bifax* is from the Graybullian. However, the referred Clarkforkian specimens are virtually identical to those from the early Wasatchian, and are referable to *A. bifax*. Though not described by Rose (1981), a mandible of *A. bifax* from the Clarkforkian has an associated upper molar (UMMP 69219) that agrees with the holotype of *A. bifax* in size and morphology.

Subfamily Pseudoparamyinae Michaux, 1964

Included genera.—*Plesiarctomys* Bravard (1850), *Pseudoparamys* Michaux (1964), and *Franimys* Wood (1962).

Discussion.—Michaux (1964, 1968) defined the Pseudoparamyinae on the following dental characters: 1) P^3 absent; 2) P^4 anteroposteriorly compressed; 3) M^1 and M^2 rectangular with protoloph and metaloph parallel; 4) anterior cingulum on lower molars developed; 5) trigonid basins closed; 6) mesoconid transversely elongate; and 7) posterior cingulum continuous with the entoconid. He included the two European genera *Pseuodoparamys* and *Plesiarctomys*. Michaux (1968) also noted the similarity between the P^4 of *Pseudoparamys* and *Franimys*.

Some features of the skull appear to be shared by *Pseudoparamys*, *Plesiarctomys*, and *Franimys*. In all three genera the posterior margin of the anterior root of the zygoma is level with the middle of P^4. It is just slightly more forward in *F. amherstensis*. If Wood's (1970: Fig. 1) reconstruction of the skull of *Plesiarctomys* were correct, it is very similar to that of *Franimys* in having a short broad snout and having the nasals end posteriorly on the same line with the premaxillaries.

In *Franimys*, a single sagittal crest runs the length of the cranium, divides at the level of the posterior margin of the orbits and runs laterally, nearly at right angles to the sagittal crest, to the lateral margin of the skull. In *Plesiarctomys* the anterior extensions of the sagittal crest are gradual but very similar to those in *Franimys*. In manitshines the anterior part of the crest begins laterally perpendicular to the sagittal crest, as in *Franimys*, but turns into a more gradual angle. The split of the sagittal crest of *Paramys delicatus* resembles that of *Franimys*, occurring far forward on the cranium, but the anterior branches of the crest diminish laterally and do not reach the lateral margin of the skull.

The skull of *Franimys* possesses postorbital processes. These are unknown on any other ischyro-

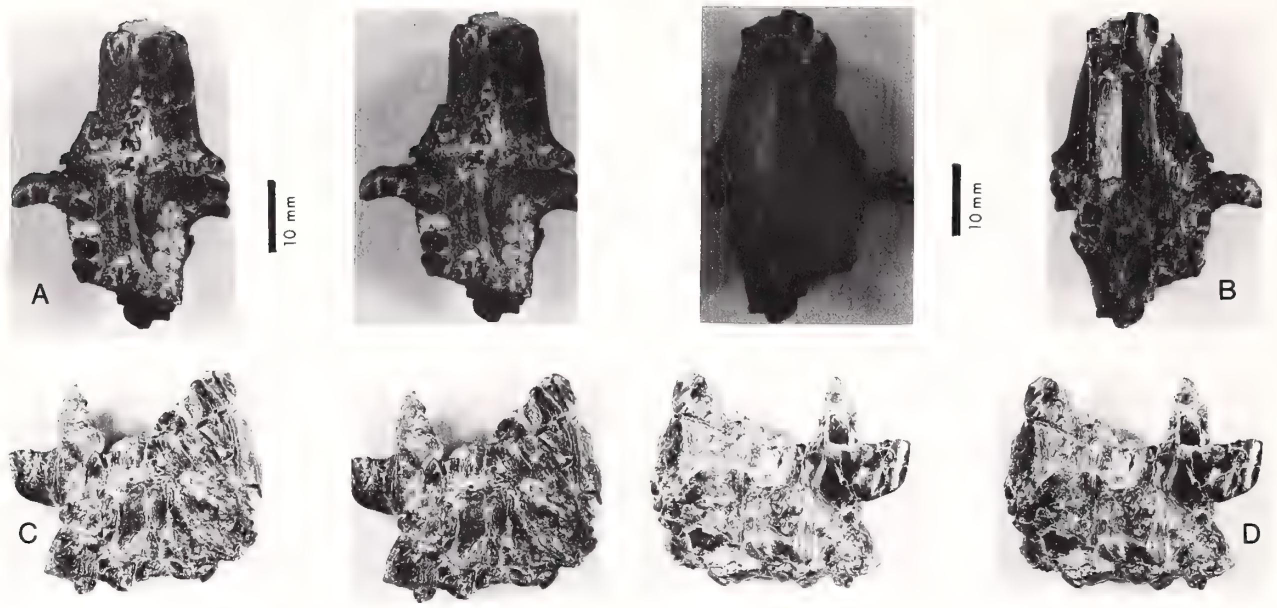


Fig. 19.—Skull of *Franimys amherstensis,* ACM 10524 (holotype). A) Stereophotograph of ventral view of the anterior portion of the skull. B) Stereophotograph of dorsal view of anterior portion of skull. C) Stereophotograph of ventral view of posterior portion of skull. D) Stereophotograph of dorsal view of posterior portion of skull.

myids except the European genus *Ailuravus* (Weitzel, 1949).

Unfortunately, no lower teeth of *Franimys* are known so no comparison can be made with those of *Pseudoparamys.*

P^4 of *Pseudoparamys* is very similar to that of *Franimys* and is two rooted. P^4 of *F. buccatus* has two buccal roots but they do not separate until well below the base of the crown. The new species of *Franimys* (described below) may have two buccal roots but all that can be determined from the known material is that there is an anteroposteriorly elongate buccal root with a central depression at the level of the alveolar margin. Once the root has entered the bone it may well divide into two. The reduction in the number of lingual roots is probably related to the anteroposterior compression of the tooth.

The only known feature of the dentition of *Franimys* that is unlike *Pseudoparamys* is the presence of P^3. However, Wood (1970) showed that in most specimens of *Plesiarctomys,* at least a dP^3 is present, indicating that *Plesiarctomys* lost P^3 independently of *Pseudoparamys.* If this criterion were dropped from Michaux's (1964, 1968) diagnosis, *Franimys* can easily be considered a pseudoparamyine.

Both Wood (1962, 1976*a*) and Black (1971) included *Franimys* in the Reithroparamyinae. However, the morphology of P^4, arrangement of the sagittal crest on the skull, and lack of a bulla ossified to the skull, separate *Franimys* from *Reithroparamys* and the Reithroparamyinae.

Franimys Wood, 1962

Type species.—*Franimys amherstensis* Wood, 1962.

Range.—Early Eocene of Wyoming and New Mexico.

Referred species.—*Franimys buccatus* (Cope, 1877) and *Franimys ambos,* new species.

Emended diagnosis.—Small rodents; broad skull with short snout; postorbital processes on the frontals; nasals and premaxillary bones extend posteriorly to the same level; posterior margin of the anterior root of the zygoma level with the center of P^4; P^4 small, narrow, oval in occlusal outline, without a hypocone; hypocone on upper molars small; I^1 disproportionately large.

Franimys amherstensis Wood, 1962
(Figs. 19, 20, 21)

Type specimen.—ACM 10524, skull with RP^4 and M^2–M^3, and mandible without teeth and several postcranial bones.

Horizon and locality.—"100 yards southeast of the northwest corner of Sec. 9, T56N, R101W" (Wood, 1974:17), Willwood Formation, Wyoming.

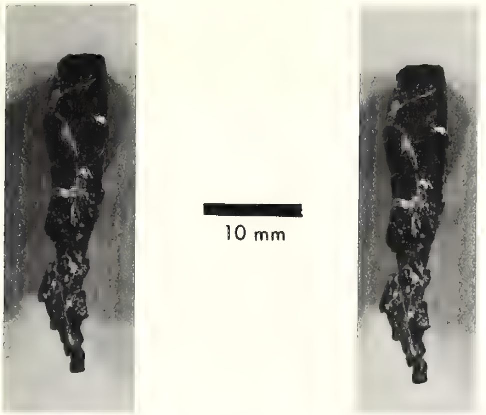


Fig. 20.—Stereophotograph of ventral view of the mandible of *Franimys amherstensis,* ACM 10524 (holotype). Anterior toward the top.

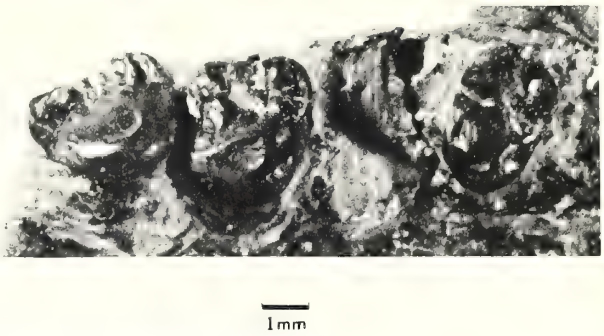


Fig. 21.—Upper cheek teeth of *Franimys amherstensis,* P^4, M^2–M^3, ACM 10524 (holotype).

Age.—Earliest Eocene (Clarkforkian).

Emended diagnosis.—Largest species of the genus; posterior margin of the anterior root of zygoma nearly even with anterior margin of P^4; P^4 very narrow anteroposteriorly and two rooted.

Discussion.—A number of features of the skull and mandible of *Franimys amherstensis* were incorrectly figured by Wood (1962: Fig. 48). The posterior half of the skull (ACM 10524) is so badly crushed that many features are either distorted or impossible to determine. The temporal foramina were figured and described by Wood as being very near the sagittal crest, a unique feature among ischyromyids. However, the fragments of bone which contain these foramina appear to be from near the temporal-squamosal boundary, as in all other ischyromyids, and to have been moved to the central position by crushing of the skull. It is also impossible to determine if an interparietal bone is present, due to extensive crushing.

The only known mandible of the species belongs to the holotype. Wood (1962) described this specimen as being incipiently hystricognathous with the angle of the mandible arising laterally from the side of the mandible. As discussed previously, this specimen is so badly crushed and partially exploded by concretionary deposition between the fragments that the true position of the angle cannot be reconstructed.

P^4 of *F. amherstensis* is anteroposteriorly compressed and two rooted. Most of the buccal margin of the tooth is broken away on the holotype. Wood (1962:142) interpreted this tooth as having a single major loph, the doubled metaloph, a thin anterior cingulum which terminated buccally with a small swelling homologous to the paracone, and a short posterior cingulum. This tooth is in such poor condition in the type that its morphology is very difficult to interpret. The buccal swelling that Wood interpreted as a paracone appears to be a wear facet that has extended onto the side of the tooth. There is no distinct swelling. More importantly, the valley between the metaloph and anterior cingulum on P^4 is a wear facet and not an original valley between these lophs. The small valley in the center of the metaloph interpreted by Wood as the valley between the two metalophs is more likely the wear facet for the metaconule. In all, it is probable that a protoloph was present on P^4 of *F. amherstensis* but has been worn away. The amount of wear on the molars is comparable with that on P^4, and sufficient to have removed the protoloph of P^4. The position and size of the paracone cannot be determined because of wear and breakage of the tooth on the holotype.

Wood (1962) interpreted the morphology of P^4 of *F. amherstensis* as primitive for all rodents. However, most other early ischyromyids have a narrow metaloph with a metacone smaller than the paracone, implying the secondary development of the metacone and metaloph, with the paracone and protoloph being primary. The primary development of the paracone and subsequent development of the metacone on the posterior upper premolars in rodents is also consistent with other orders of mammals such as insectivores and primates.

Even though the morphology of the occlusal surface of P^4 is very poorly known, *F. amherstensis* is distinguishable from other species of *Franimys* by its size and slightly more anterior position of the anterior root of the zygoma.

The upper incisor of *F. amherstensis* is larger in relation to the size of the cheek teeth than in other

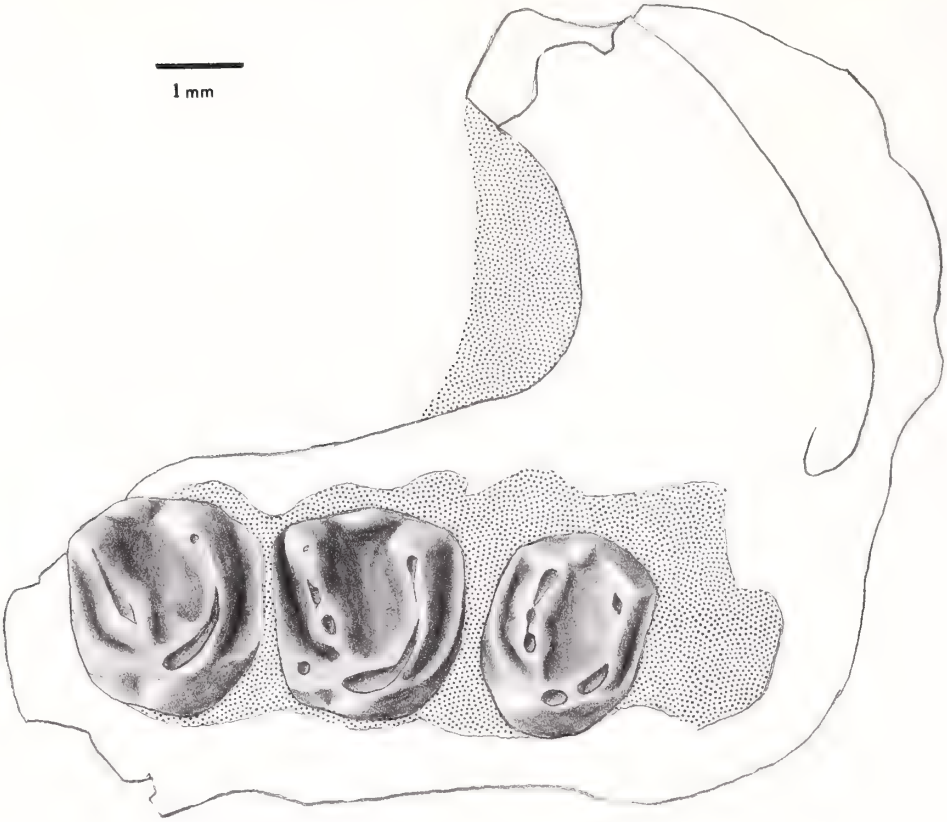


Fig. 22.—Holotype of *Franimys ambos,* RP^4–M^2, CM 37091.

ischyromyids. The enamel on the upper incisors is almost completely restricted to the anterior surface. It does not extend onto the lateral surface as far as in *Paramys copei.*

Franimys buccatus (Cope, 1877)

Plesiarctomys buccatus Cope, 1877.
Paramys buccatus (Cope) Roger, 1896.
?*Sciuravus buccatus* (Cope) Matthew, 1909.
"*Paramys*" *buccatus* (Cope) Wilson, 1949.
Franimys buccatus (Cope) Wood, 1962.

Type specimen.—USNM 1129, right maxilla with P^4–M^2.

Horizon and locality.—Unknown locality, San Jose Formation, New Mexico.

Age.—Probably middle or late early Eocene (Lysitean or Lostcabinian).

Emended diagnosis.—Small species; paracone of P^4 situated near center of the tooth; M^1 distinctly smaller than M^2.

Discussion.—*Franimys buccatus,* like *F. amherstensis,* is known only from the holotype. It differs from the type species in being slightly smaller. Because the occlusal pattern of P^4 of *F. amherstensis* is not clearly known, no comparison can be made with that of *F. buccatus.* The position of the paracone on P^4 of *F. buccatus* is unique among ischyromyids. The much smaller size of M^1 relative to M^2 is also distinctive.

Franimys buccatus is clearly referable to *Franimys* based on its small size, position of the anterior root of the zygoma, and the small oval P^4, lacking a hypocone.

Franimys ambos, new species
(Fig. 22, Table 9)

Type specimen.—CM 37091, right maxilla with P^4–M^2.

Horizon and locality.—Type area of the Lysite Member, Wind River Formation, Wyoming.

Age.—Middle early Eocene (Lysitean).

Diagnosis.—Smallest species of the genus; P^4 with complete protoloph connecting to a buccally positioned paracone; M^1 and M^2 nearly equal in size and squre in outline.

Hypodigm.—Type only.

Etymology.—*ambos*, Greek, rim.

Description.—*Franimys ambos* is smaller than either *F. buccatus* or *F. amherstensis.* The anterior root of the zygoma is slightly more posterior than in the other species, but in all other features of the palate observable, is identical with those of the other species.

P^3 is absent in the holotype but it is evident from the alveolus and wear facet on P^4 that P^3 was small and situated near the center of the anterior margin of P^4.

P^4 is more molariform than in *F. buccatus.* The paracone is nearly at the buccal edge of the tooth. The protoloph connects the paracone to the protocone, but there is no indication of a protoconule on it. A separate wear facet is present on the anterobuccal slope of the protocone but this is not a protoconule. The anterior cingulum runs lingually from the level of the paracone to the level of the apex of the protocone and is closely appressed to the protoloph. The metacone is anteroposteriorly compressed, and the metaconule is double. The lingual metaconule is larger than the more buccal one. The metaloph attaches to the protocone via a low narrow loph. The posterior cingulum originates at the protocone and wraps around the posterior margin of the tooth, ending buccally at the metacone. There is no indication of a hypocone. A small mesostyle is present and placed nearer the metacone than paracone.

M^1 and M^2 are nearly identical in size and proportions. They do not differ from the other species of the genus except for smaller size and apparent lack of a protoconule on the protoloph. Size and position of the hypocone, anteroposterior elongation of the mesostyle and length and arrangement of the cingula and metaloph are identical to those of *F. buccatus* and *F. amherstensis.*

Discussion.—*Franimys ambos* is the smallest species of the genus. M^1 and M^2 of *F. ambos* are nearly identical in size and proportions, unlike *F. buccatus* in which M^1 is markedly smaller than M^2. P^4 of *F. ambos* most closely resembles that of *Pseudoparamys teilhardi* (Michaux, 1968: Pl. 4, Fig. 1). The paracone is situated at the buccal margin of the tooth and there is a complete protoloph, as in *P. teilhardi.* P^4 of *F. ambos* differs from that of *P. teilhardi* in being less compressed anteroposteriorly.

The molars of *F. ambos* are very close in morphology to those of both *F. amherstensis* and *F. buccatus* in having an anteroposteriorly elongate mesostyle, poorly developed protoconule, and small hypocone. No specimens of lower molars from the Lysite Member of the Wind River Basin are comparable in size to the type of *F. ambos.* Therefore, *Franimys* is still known only from upper dentitions.

Subfamily Ailuravinae Michaux, 1968

Included genera.—*Ailuravus* Rütimeyer (1891), *Melidimys* Michaux (1968), and *Mytonomys* Wood (1956).

Table 9.—*Dental measurements of the type specimen of* Franimys ambos *(in millimeters), CM 37091.*

Tooth	a–p	tra	trp
P^4	1.85	2.51	—
M^1	2.23	2.51	2.48
M^2	2.19	2.47	2.31

Discussion.—*Michaux* (1968) first named the Ailuravinae and included the European genera *Meldimys, Ailuravus* and *Maurimontia* (=*Ailuravus,* Wood, 1976*b*). Later, Wood (1976*b*) suggested that the North American genus *Mytonomys* should be included in this subfamily. His diagnosis for the subfamily is accepted here and does allow for the inclusion of early Eocene species of *Mytonomys* described below.

The late Eocene genus *Eohaplomys* Stock (1935) from California which has been traditionally considered an aplodontid (Wilson, 1949), has recently been shown to be more distantly related to the earliest aplodontids and is not considered an aplodontid at all (Rensberger, 1975). There is some similarity between *Eohaplomys* and late Eocene *Ailuravus* (see Wood, 1976*b*) but a complete study of both genera must be undertaken in order to determine of there is any special relationship between them.

Mytonomys Wood, 1956

Type species.—*Mytonomys robustus* (Peterson, 1919).

Range.—Early Eocene to earliest Oligocene, Wyoming, Colorado, California, Utah, and Mexico.

Included species.—*M. burkei* (Wilson, 1940), *M. coloradensis* (Wood, 1962), *M. wortmani* (Wood, 1962), and *M. gaitania* Ferrusquia and Wood, 1969.

Emended diagnosis.—Posterior margin of anterior root of zygoma level with middle of M^1; P^4 expanded buccally, nearly circular in outline with distinct conules and no hypocone; molars long with anterior cingulum widely separated from protoloph; hypocone distinct with notches present on either side of protocone lingually; mesostyle on upper molars large or multiple, extending lingually into central basin; buccal margin of M^1–M^2 convex at paracone; lower molars with broad accessory crenulations running into talonid basin; trigonid basins minute; M_3 elongate; posterolophid on lower molars distinct and separated from entoconid at least on M_2; partial hypolophid present on M_1–M_2.

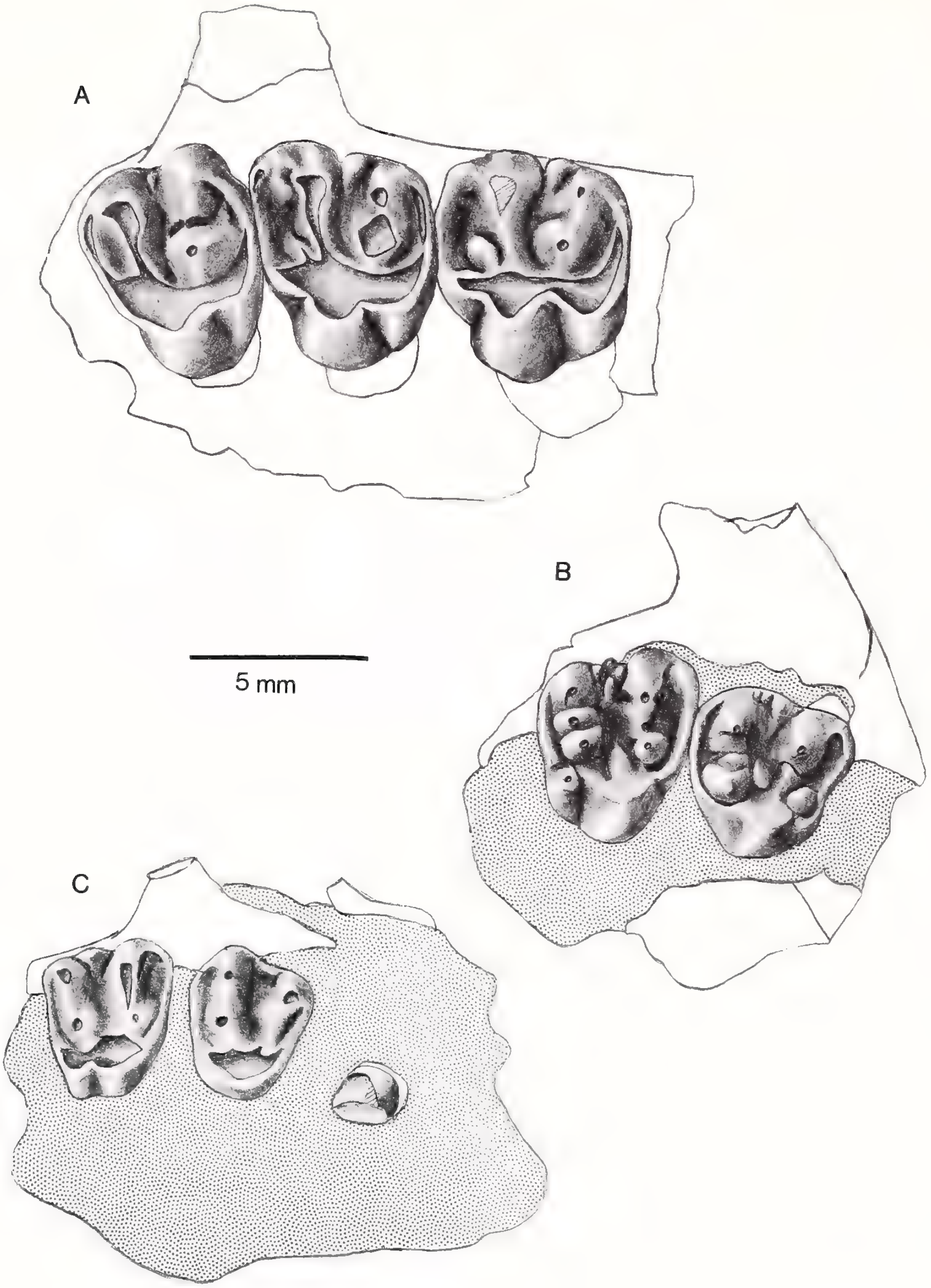


Fig. 23.—Upper dentitions of *Mytonomys*. A) *M. robustus*, LP^4–M^2. B) *M. coloradensis*, RP^4–M^1, FMNH P 26596, holotype. C) *M. wortmani*, RP^3–M^1, CM 22208.

Mytonomys coloradensis (Wood, 1962)
(Figs. 23b, 24b)

Pseudotomus coloradensis Wood, 1962.
Leptotomus loomisi Wood, 1962.

Type specimen.—FMNH P 26596, two maxillary fragments with RP^4–M^1 and LM^1–M^2.

Horizon and locality.—Type from the Lysite equivalent, Debeque Formation, Colorado. Referred specimens from the Lysite Member, Wind River Formation and from the Gray Bull, Lysite and possibly Lost Cabin levels, Willwood Formation, Wyoming.

Age.—Early, middle and possibly late early Eocene (Graybullian to ?Lostcabinian).

Referred specimens.—ACM 2568, CM 36086, ACM 335a (from Lysite Member, Wind River Formation); FMNH P 26788 (from Debeque Formation); AMNH 4966, 4968, 55946, 55948 (from Graybullian or Lysitean, Willwood Formation); and AMNH 15138 (from ?Lostcabinian, Willwood Formation).

Emended diagnosis.—Mesoconid large and crenulations present but relatively low on lower molars; metaconules on upper cheek teeth multiple; lingual notch anterior to protocone on M^2 less distinct than the posterior notch; anterior cingulum on P^4 restricted to parastylar area; P_4 nearly equal in size to M_1; I_1 relatively narrow and parallel sided.

Discussion.—Wood (1962) originally assigned *Mytonomys coloradensis* to *Pseudotomus.* However, *M. coloradensis* differs from *Pseudotomus* in having longer upper molars, more complex occlusal pattern on the molars, narrow lower incisor, more posterior position of the zygoma, lighter and more slender mandible. *Quadratomus* is the only manitshine with a lower incisor and position of the zygoma similar to those of *M. coloradensis. Quadratomus* differs from *M. coloradensis* in having broad shallow basins on all molars and a heavy mandible, lacking the irregularities of the enamel as in *Mytonomys,* and having a specialized manitshine zygoma. There are no characters of *M. coloradensis* that suggest that it is related to any manitshine.

The type of *M. coloradensis* (FMNH P 26596) is two associated maxillae with right P^4–M^1 and left M^1–M^2. The features that unite this specimen with upper dentitions of late Eocene *Mytonomys* (Black, 1968*b*) are: 1) P^4 nearly circular in outline, lacking a hypocone; 2) prominent wrinkling of enamel on the molars; 3) buccal margin of the molars convex above the paracone; 4) mesostyle complex with small lingual extension; 5) notches on the lingual margin of M^1–M^2 anterior and posterior to the protocone; and 6) posterior margin of the anterior root of the zygoma above the middle of M^1. The multiple metaconule on M^1–M^2 of *M. coloradensis* is not present on *M. robustus* from the late Eocene.

All of the lower dentitions referred by Wood (1962) to *M. coloradensis* are heavily worn and little can be determined about their occlusal morphology except that the entoconid is separated from the posterolophid on M_2. The lower incisor of *M. coloradensis* closely resembles that of *Quadratomus* except that the sides are more nearly parallel.

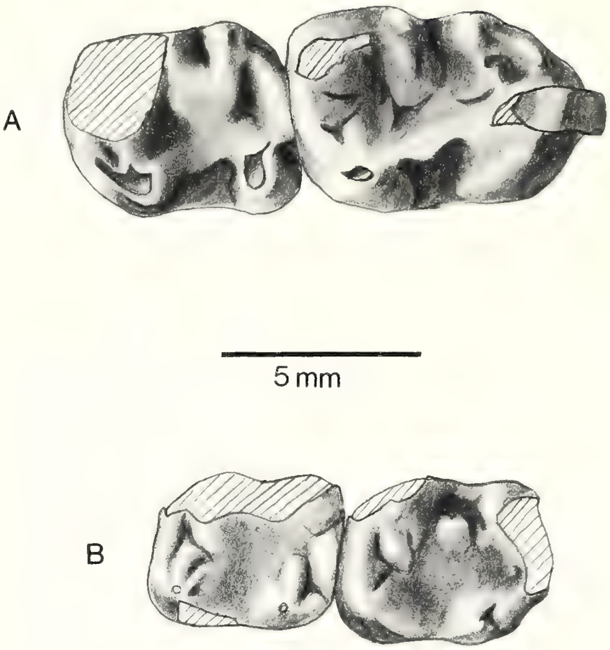


Fig. 24.—Lower dentitions of *Mytonomys.* A) *M. robustus,* LM_2–M_3, FMNH 8786. B) *M. coloradensis,* RM_2–M_3, ACM 335a (=holotype of *Leptotomus loomisi*).

The holotype of *Leptotomus loomisi* (ACM 335a) agrees in size of the molars and morphology of the lower incisor with referred specimens of *M. coloradensis.* The I_1 of *M. coloradensis* figured by Wood (1962a: Fig. 58d) has a narrow flattened area on the anterior surface. The anterior surface of I_1 of *L. loomisi* and other referred specimens of *M. coloradensis* is rounded. This is a minor variation in the morphology of the lower incisor and is also variable in species of *Paramys, Reithroparamys,* and *Acritoparamys.*

The type of *L. loomisi* agrees with late Eocene species of *Mytonomys* in having: 1) low, broad irregularities on the molars; 2) a short, low hypolophid running from the entoconid; 3) distinct buccolingually elongate hypoconulid on M_2; 4) posterolophid separated from the entoconid on M_2; and 5) M_3 elongate. The lower teeth of *M. coloradensis,* including *L. loomisi,* differ from those of late Eocene *Mytonomys* in having a P_4 approximately equal in size to M_1, more pronounced mesoconid with a weak ectolophid, and narrow I_1.

Black (1968*b*) commented that there was no separation between the posterolophid and the entoconid on the lower molars of *M. robutsus,* and that the entoconid just rose high above the level of the posterolophid. However, the entoconid is separated at least on M_2 of all species of *Mytonomys.*

Because no associated upper incisors of *M. coloradensis* have been recovered, the isolated incisors previously identified as this species from the Lost Cabin Member, Wind River Formation (Wood, 1962; Guthrie, 1971) should not be referred to this species.

Wood (1962: Tables 27, 58, 60) provided dental measurements of *Mytonomys coloradensis.*

Mytonomys wortmani (Wood, 1962)

(Fig. 23b)

Type specimen.—AMNH 4761, associated mandibles with LP_4–M_2 and RM_1–M_3 and some associated postcranial bones.

Horizon and locality.—Type and all referred specimens from type area of the Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—WAM 6001, CM 22208.

Emended diagnosis.—Smallest species of the genus; protoloph weakly developed on P^4; P_4 smaller than M_1; posterolophid separated from entoconid on P_4–M_2; accessory crenulations weakly developed on molars.

Description.—The posterior margin of the zygoma of *M. wortmani* is level with the center of M^1. The infraorbital foramen is small. Only part of the border of the infraorbital foramen is preserved on one specimen (CM 22208) so that the exact size of the infraorbital foramen cannot be determined.

P^3 is typically single rooted and peg-like. It is slightly larger relative to P^4 than is the case of *Paramys copei.* Nothing can be said about the morphology of the occlusal surface of P^3, since the only known specimen is heavily worn.

P^4 is submolariform and slightly smaller than M^1. The paracone is far anterior and lingual to the metacone which creates a broad low valley which runs buccolingually across the tooth. The paracone attaches directly to the protocone by way of a broad, short protoloph. There is no indication of a protoconule. The anterior cingulum runs about half the width of the tooth from the apex of the paracone buccally to the anterobuccal extent of the protocone. The metacone is anteroposteriorly compressed. The circular metaconule is nearly as large as the metacone. The metaloph runs anterolingually and joins the protoconid. The posterior cingulum extends the entire width of the tooth. Only a minute mesostyle is present between the metacone and paracone. There are some irregularities on the surface of the enamel.

M^1 is the only upper molar known from *M. wortmani.* The buccal border of the tooth is convex in the parastylar area. The anterior cingulum is widely separated from the paracone but runs posterolingually, joining the protocone buccal to the lingual margin of the tooth. This feature makes the tooth shorter lingually than bucally. The paracone and metacone of M^1 are subequal in size and compressed anteroposteriorly. The protoloph runs directly lingual with a distinct protoconule just buccal to the protocone. The metaloph runs anterolingually to the protocone. The metaconule is larger than the protoconule and placed lingually on the metaloph. The posterior cingulum is closely appressed to the metaloph and runs the entire width of the tooth. There is a large mesostyle which extends into the valley between the metacone and paracone. As in P^4, there are some minor irregularities on the enamel surface.

Discussion.—Wood (1962) described *Paramys wortmani* on the basis of lower dentitions and a few postcranial bones. Guthrie (1971) synonymized *P. wortmani* with *P. copei,* stating that the differences between these two species were within the bounds of variation of a species. However, it does seem that the separation of the entoconid from the posterolophid on the lower cheek teeth, slightly larger size, and wider I_1, clearly separate *M. wortmani* from *P. copei.*

A maxilla with P^3–M^1 (CM 22208) from the Lost Cabin Member, Wind River Formation is here referred to *M. wortmani* based on its slightly larger size than *P. copei* and morphology of the cheek teeth and position of the zygoma that more nearly resemble other species of *Mytonomys.*

The holotype of *M. wortmani* is very heavily worn so many features are obscured, but still there are similarities to late Eocene *Mytonomys.* Wood (1962: 37) noted that there were irregularities on the enamel of the molars but suggested that these indicated affinities with *Thisbemys.* The crenulations on M_3 of the holotype of *M. wortmani* are barely recognizable but appear to be broader than those of *Thisbemys,* more nearly approaching other species of *Mytonomys* in this feature. The separation of the entoconid on P_4–M_2 of *M. wortmani* also allies it with *Mytonomys.* There appears to be a short, low hypolophid running into the talonid basin from the entoconid of M_1–M_2 of *M. wortmani,* as in other *Mytonomys.* This feature is also obscured by wear and the original length and height of this loph cannot be determined.

The maxilla referred to *M. wortmani* differs from those of *Paramys* and is similar to other *Mytonomys* in several features: 1) posterior margin of anterior root of the zygoma level with center of M^1; 2) P^4 expanded anteriorly giving the tooth a more nearly circular occlusal outline; 3) M^1 elongate anteroposteriorly; 4) anterior cingulum of M^1 widely separated from protoloph; 5) buccal margin of M^1 at paracone convex; and 6) hypocone on M^1 large, creating a deep notch on the lingual margin of the tooth between it and the protocone.

M. wortmani differs from other species of *Mytonomys* in having a relatively smaller P_4 that is very narrow anteriorly, having less pronounced irregularities on the enamel of the molars, having the entoconid separated from the posterolophid on M_1, having P^4 less circular in occlusal outline, and having only a faint notch on the lingual margin of M^1 anterior to the protocone.

In all of these features, *M. wortmani* is more primitive than *M. coloradensis* and the late Eocene species of *Mytonomys.* The double metaconule on the upper molars and narrower I_1 of *M. coloradensis* remove it from an ancestral position to later species of the genus. *Mytonomys wortmani* has the primitive single metaconule on the upper molars and an I_1 that is widest anteriorly, resembling I_1 of *Paramys copei.* There are no features which would remove *M. wortmani* from representing an ancestral stock for all later *Mytonomys.*

Two specimens listed by Wood (1962: 36) in the hypodigm for *M. wortmani* (AMNH 4760b, AMNH 4760c) are referable to *P. copei.*

Family Sciuravidae Miller and Gidley, 1918

Sciuravus Marsh, 1871

Type species.—Sciuravus nitidus Marsh, 1871.

Sciuravus wilsoni Gazin, 1961

Type specimen.—USNM 22425, right mandible with P_4–M_2.

Horizon and locality.—Type and referred specimen from center of T29N, R91W, Sublette County, Knight Member, Wasatch Formation, Wyoming. Other referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Wyoming.

Age.—Late to latest early Eocene (Lostcabinian to Gardnerbuttean).

Referred specimens.—USNM 22424 (from Knight Member) and PU 17785 (from Cathedral Bluffs).

Discussion.—No additional specimens of *Sciuravus wilsoni* have been described since Gazin's (1961, 1962) description of the species. The isolated teeth from the Cathedral Bluffs Tongue referred to *S. wilsoni* (PU 17785, previously cited as PU 16109) consist of P_4, M_1, two M_2s, and two M_3s. An M_2 of *Knightomys depressus* is also included with these specimens. The molars included in PU 17785 are slightly larger than those of the holotype (Gazin, 1962: 50) but distinctly smaller than the original sample of the Bridgerian species *S. nitidus* reported by Wilson (1938:133). West (1973: Table 27) listed measurements for a large sample of *S. nitidus.* The size ranges listed overlapped the sizes of both *S. nitidus* and *S. wilsoni.* West, however included specimens from the Cathedral Bluffs Tongue and the Bridger Formation in his table, and may have mixed the two species of *Sciuravus* in his sample thus giving an erroneous size range for *S. nitidus.* In all other samples, *S. wilsoni* is smaller than *S. nitidus.*

Knightomys Gazin, 1961

Type species.—Knightomys senior (Gazin, 1952).

Range.—Early Eocene of Wyoming, Colorado, and New Mexico.

Referred species.—K. depressus (Loomis, 1907), *K. huerfanensis* (Wood, 1962) and *K. minor* (Wood, 1965).

Emended diagnosis.—Small sciuravids; single sagittal crest on skull; anterior zygomatic root arises anterior to P^4; masseteric fossa on mandible ends anteriorly below posterior margin of M_1; second minute mental foramen present on mandible; cheek teeth cuspate with rudimentary loph development; protoloph and metaloph complete and separate on upper molars; entoconid on lower molars isolated with incomplete hypolophid entering into talonid basin; mesoconid distinct on lower molars and extends posterolingually into the talonid basin on M_2–M_3; minute metastylid present on lower cheek teeth.

Discussion.—Knightomys was named by Gazin (1961) for *Tillomys senior* Gazin (1952) from the early Eocene Knight Member of the Wasatch Formation. Wood (1965) recognized that *Sciuravus depressus* Loomis (1907) from the Lysite Member of the Wind River Formation was referable to Gazin's genus and described the skull of *Knightomys,* basing this description of the holotype of *K. depressus* (ACM 432), a badly crushed partial skull. A number of Wood's observations appear incorrect based on additional skull material of *K. depressus* and *K. huerfanensis.*

The skull of *Knightomys* most closely resembles the skull of *Sciuravus* (Wood, 1965; Dawson, 1961) but is more elongate with a less inflated cranium. A low sagittal crest runs from the posterior margin of the skull and divides posterior to the orbits at the point of maximum postorbital constriction. The point of bifurcation of the sagittal crest varies on the known skulls of *Knightomys* but is generally near the same point as in *Sciuravus* (Dawson, 1961). Supraorbital ridges are developed in *Knightomys* somewhat more so than in *Sciuravus.*

The zygoma is thin and the scar on its ventral

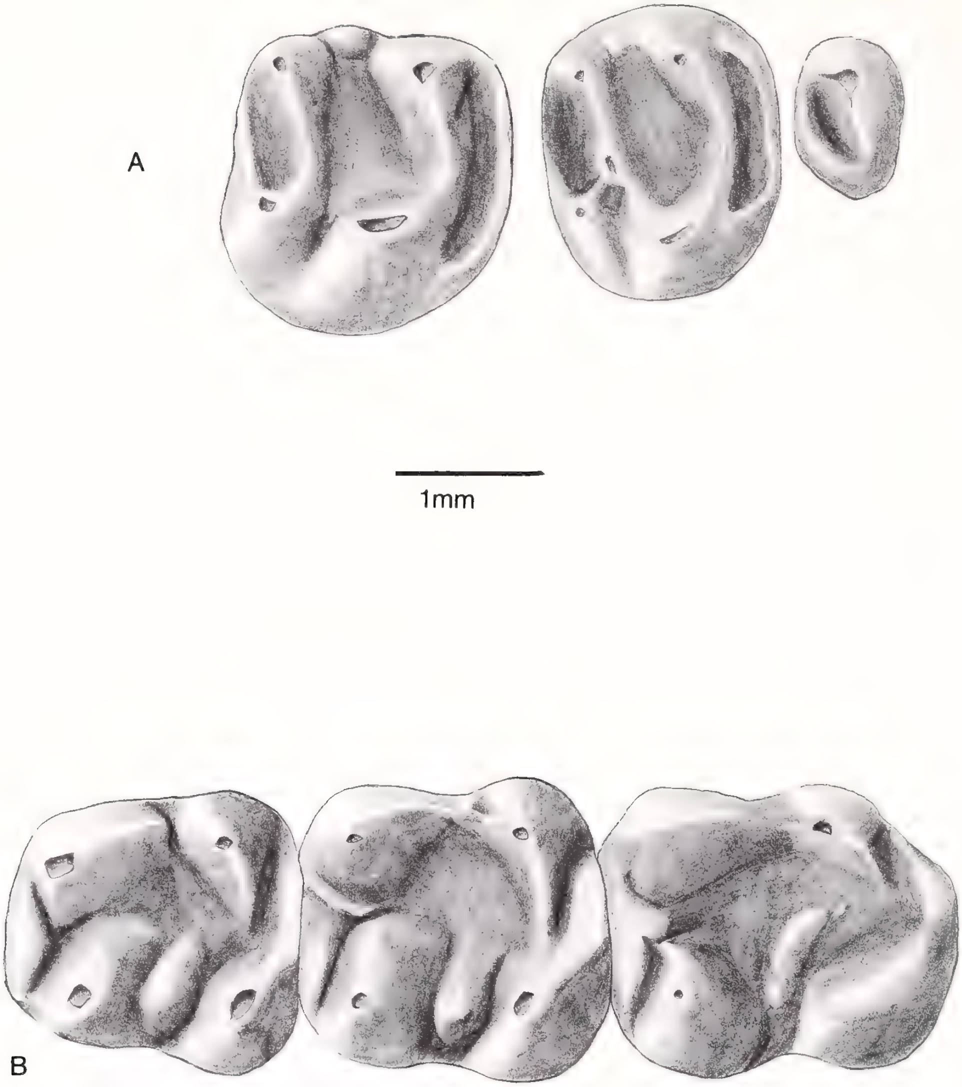


Fig. 25.—Cheek teeth of *Knightomys depressus.* A) RP^3–M^1, KU 16564. B) LM$_1$–M$_3$, CM 21155.

side for the attachment of the masseter muscle is limited to the anterior root. The posterior margin of the anterior root of the zygoma is even with the anterior margin of P^4, as in *Sciuravus* and *Microparamys.*

Contrary to Wood (1965), the infraorbital foramen of *Knightomys* (known for both *K. depressus,* AMNH 55112, and *K. huerfanensis,* CU 29944) is small. It is equal in relative size to that of *Sciuravus.* The skull on which Wood based his observations is badly damaged and the infraorbital foramen, artificially enlarged. No other foramina except the incisive foramina and foramen magnum are preserved on any of the skulls of *Knightomys.* The basicranial region is also not preserved on any of these specimens.

The pattern of sutures on the skull of *Knightomys* are virtually identical to those of *Sciuravus* (see Dawson, 1961; Wahlert, 1974). However, the present skull material of *Knightomys* does not allow determination of the presence or size of an interparietal bone. Any other specific features of the skull will be discussed under the separate species of *Knightomys.*

Knightomys depressus (Loomis, 1907)
(Fig. 25, Table 10)

Sciuravus depressus Loomis, 1907.

?*Sciuravus depressus* Loomis, Troxell, 1923.
"*Sciuravus*" *depressus* Loomis, Gazin, 1962.
Microparamys lysitensis Wood, 1962.
Microparamys cathedralis Wood, 1962.
Knightomys depressus (Loomis) Wood, 1965.

Type specimen.—ACM 432, partial skull with RM^1–M^3.

Horizon and locality.—Type and some referred specimens from the type area of the Lysite Member of the Wind River Formation, Wyoming. Other referred specimens from Lost Cabin Member, Wind River Formation, Wyoming; Lysite equivalent of Debeque Formation, Colorado; Upper Huerfano Formation (localities II and III), Colorado; Cathedral Bluffs Tongue, Wasatch Formation, Wyoming; and the Largo Member, San Jose Formation, New Mexico.

Age.—Middle to latest early Eocene (Lysitean to Gardnerbuttean).

Referred specimens.—ACM 458, 487, 2951b, 2951d, 2952, 2962, 2966, 2974, 4388, 4389, CM 21791, 22847–22849, 28741, 35937, 36091, 37089, 37093, 37094, KU 16564, AMNH 12767 from Lysite Member). CM 21151–21155, 21160, 21162, 22244–22248, 22250–22252, 22254, 26503, 26514–26518, 29153–29157, 29159, 29164, 35860–35862, 36517–36522, 36524, 36525, 36528–36530, 36920–36922, 37253, 37254, CU 44359, 44368, 44706, 44715, 44837, 44841, 44845, 45218, 45221, 45225, 45328, 45358, 45068, 42825, 42857, PU 17252 (from Lost Cabin Member). FMNH PM 1226, P 26587 (from Debeque Formation). AMNH 55112, 55142, 55144, 55194, 55988, YPM 16473, CU 2148, CU 26542, 32752, 32785, 33276, 29944 (from Upper Huerfano, localities II and III). YPM 16512 (from Largo Member). PU 16112, FMNH PM 15895 (from Cathedral Bluffs Tongue).

Emended diagnosis.—Intermediate sized member of the genus; anterior cingulum separated from protoconid and metaconid on unworn lower molars; hypolophid variable in length and disappears rapidly with moderate wear on lower molars; P^4 with hypocone minute; posterolingual lophid of mesoconid of M$_3$ very broad, extending to posterolophid.

Discussion.—The only tooth of *Knightomys depressus* not previously described is P^4. This tooth is small relative to M^1, has a complete protoloph and metaloph, which converge anteriorly at the protocone. There is no trace of a protoconule on the protoloph, but a distinct metaconule is present. Both anterior and posterior cingula run the entire width of the tooth. The hypocone is variable in size and always present. There is no mesotyle on P^4.

Knightomys depressus differs from all other species of the genus in its size. It differs from *K. minor* and *K. senior* in having separation of the anterior cingulum from the protoconid on the lower molars and the minor swelling of the anterior cingulum buccally.

Table 10.—*Dental measurements of* Knightomys depressus *(in millimeters).*

Measurements		N	M	S	V	OR
P_4–M_3		5	7.75	.23	2.9	7.39–7.97
P_4	a–p	18	1.69	.09	5.3	1.56–1.88
	tra	15	1.27	.09	7.1	1.11–1.42
	trp	16	1.49	.10	6.8	1.35–1.69
M_1	a–p	41	1.82	.08	4.4	1.67–2.00
	tra	37	1.51	.09	6.1	1.33–1.63
	trp	39	1.70	.10	6.2	1.44–1.89
M_2	a–p	43	1.88	.08	4.2	1.70–2.02
	tra	39	1.73	.08	4.8	1.59–1.92
	trp	41	1.84	.09	4.7	1.72–1.98
I_1	a–p	10	2.18	.20	9.3	1.70–2.49
	tra	10	1.28	.10	8.2	1.14–1.43
P^3	a–p	4	0.70	—	—	0.55–0.78
	tra	4	0.78	—	—	0.52–0.95
P^4	a–p	8	1.49	.12	8.4	1.31–1.68
	tra	8	1.73	.14	8.4	1.52–1.91
	trp	8	1.66	.15	9.1	1.43–1.90
M^1	a–p	10	1.72	.07	4.1	1.60–1.81
	tra	10	1.88	.11	5.7	1.72–2.08
	trp	10	1.78	.11	6.1	1.66–1.99
M^2	a–p	14	1.82	.12	6.8	1.57–2.03
	tra	14	2.00	.14	7.0	1.69–2.22
	trp	14	1.82	.12	6.8	1.59–2.01
M^3	a–p	2	1.80	—	—	1.66–1.93
	tra	3	1.81	—	—	1.74–1.93
I^1	a–p	2	2.68	—	—	2.26–3.10
	tra	2	1.43	—	—	1.26–1.59

Contrary to Wood's (1965) observations, the metaconule on the upper molars is not connected to the protocone and hypocone by lophs of equal height. Only in the holotype (ACM 432) is there any connection between the protocone and metaconule, and on this specimen it occurs only on M^2 via an extremely weak loph. This connection is an artifact of very heavy wear of the tooth of the holotype, and the metaconule wear facet has merged with the facet of the protocone. Gazin's (1962: Pl. 5, Fig. 8) figure of this specimen clearly shows the separation of the protoloph from the metaloph.

Guthrie (1971) referred two of Wood's (1962) species, *Microparamys lysitensis* and *M. cathedralis*, to *K. depressus* because the only differences separating these species from *K. depressus* was the stage

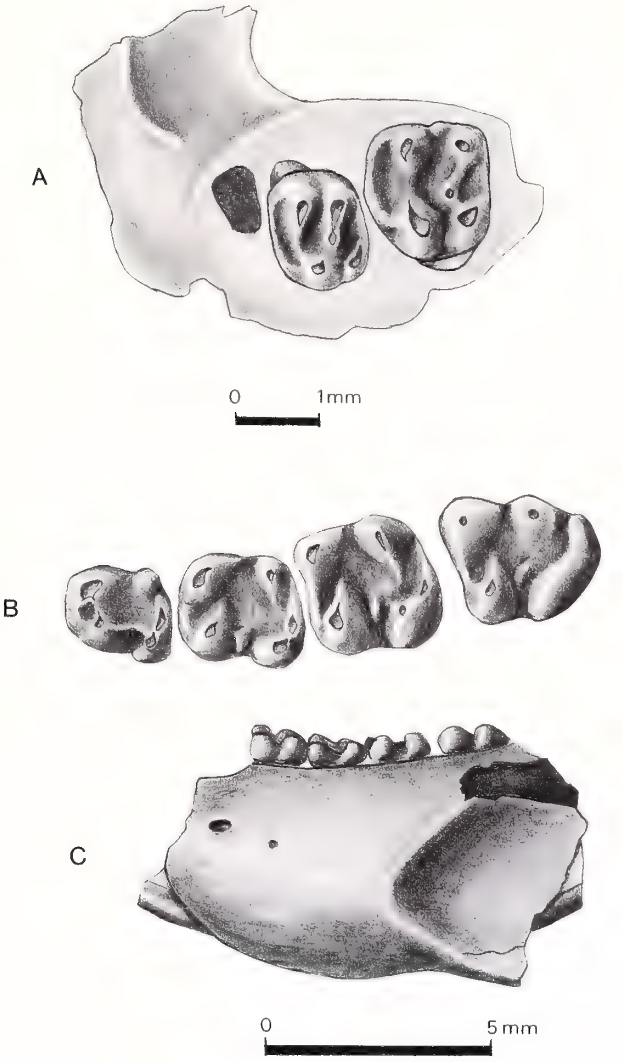


Fig. 26.—Associated upper and lower cheek teeth of *Knightomys minor,* CM 36090. A) LP^4–M^1. B) LP_4–M_3. C) Lateral view of mandible.

of wear of the tooth. Wood (1962: Fig. 54o) noted the unique shape of I_1 of *M. cathedralis* as a specific character. However, I_1 of the type of *M. cathedralis* is much more parallel sided than figured by Wood, and does not differ from that of *K. depressus.*

Knightomys depressus is the most common sciuravid in the early Eocene. No differences in size or morphology can be found between specimens of *K. depressus* from its earliest occurrence (Lysitean) through its latest (Gardnerbuttean).

Knightomys minor (Wood, 1965)
(Fig. 26, Table 11)

Dawsonomys minor Wood, 1965.

Type specimen.—ACM 4387, left mandible with P_4–M_3.

Horizon and locality.—Type and some referred specimens from the type area of the Lysite Member, Wind River Formation, Wyoming. Other referred specimens from Lysite equivalent Debeque Formation, Colorado.

Age.—Middle early Eocene (Lysitean).

Referred specimens.—CM 35927, 36089, 36090, 37095–37097, PU 17257 (from Lysite Member). FMNH PM 1229, PM 1223, P 26502 (from Debeque Formation).

Emended diagnosis.—Smallest species of genus; anterior cingulum on the lower molars narrow and connected to the protoconid and metaconid; small cuspule present in center of anterior cingulum on M_1; no anterior cingulum on P_4.

Discussion.—Wood (1965) named *Dawsonomys minor* from the Lysite beds of the Wind River Formation on the basis of a mandible with P_4–M_3. He referred his new species to *Dawsonomys* because of the nearly complete hypolophid on the molars. Additional specimens of this species, including associated upper and lower dentitions, show that this species is referable to *Knightomys.*

Knightomys minor differs from *Dawsonomys* in having: 1) less lophate teeth; 2) hypolophid on molars weak and variable in length; 3) trigonid of the lower molars not compressed or elevated; 4) large distinct mesoconid on M_1–M_3; 5) narrower I_1; and 6) a doubled mental foramen on the mandible. The lower teeth of *K. minor* resemble those of other species of *Knightomys* in all these features. The degree of loph development in *K. minor* is equal to that in *K. senior* and *K. depressus.* The mesoconid on M_2 and M_3 has a loph arising from it which runs posterolingually into the talonid basin, also as in other species of *Knightomys.* The upper molar of *K. minor* does not differ from those of *K. depressus* except in being smaller. The hypocone on P^4 is relatively large in *K. minor,* equivalent to the size of the hypocone on P^4 of *K. depressus.*

Knightomys minor is distinguishable from all other species of the genus by its smaller size and attachment of the anterior cingulum to the protoconid on the lower molars. A specimen from the type area of *K. minor* (CM 36091) consists of the anterior portion of the rostrum with both upper incisors, which are of appropriate size to be assigned to *K. minor* and have a similar cross-sectional shape to those in *K. depressus* (see Wood, 1965: Text-fig. 2e). The unique feature of this specimen is that the left

Table 11.—*Dental measurements of* Knightomys minor *(in millimeters).*

		CM 37096	CM 36090	CM 36089	CM 37097	CM 37095	ACM 4387*	FMNH P26502	CM 36090	FMNH PM 1229	FMNH PM 1223
P_4	a–p	1.32	1.26				1.18	1.30			
	tra	1.09	0.91				0.98	1.00			
	trp	1.23	1.10				1.15	1.10			
M_1	a–p	1.31	1.50	1.42			1.44	1.39			
	tra	1.12	1.23	1.22			1.17	1.19			
	trp	1.23	1.33	1.39			1.33	1.34			
M_2	a–p		1.54	1.54	1.61	1.45	1.40	1.49			
	tra		1.41	1.41	1.45	1.44	1.34	1.47			
	trp		1.46	1.47	1.51	1.49	1.38	1.59			
M_3	a–p		1.74				1.67	1.59			
	tra		1.44				1.39	1.45			
	trp		1.39				1.30	1.33			
P_4–M_3			6.16				5.70	6.05			
P^4	a–p								1.19		
	tra								1.40		
	trp								1.29		
M^1	a–p								1.43	1.41	1.31
	tra								1.60	1.65	1.43
	trp								1.45	1.59	1.33

* Taken from Wood (1965: Table 3).

incisor is rounded and smooth anteriorly, as in *K. depressus,* but the right I^1 has a minute groove that runs the entire length of the tooth. This groove is not broad and shallow, a feature relatively common on I_1 of many ischyromyids but is very narrow.

Knightomys senior (Gazin, 1952)
(Fig. 27, Table 12)

Tillomys senior Gazin, 1952.
Knightomys senior (Gazin) Gazin, 1961.

Type specimen.—USNM 19308, right mandible with P_4–M_2.

Horizon and locality.—Type from LaBarge (Gazin, 1952:6), Knight Member, Wasatch Formation, Wyoming. Referred specimens from the Lost Cabin Member, Wind River Formation, Wyoming; and possibly the Almagre Member, San Jose Formation, New Mexico.

Age.—Late and possibly middle early Eocene (Lostcabinian and possibly Lysitean).

Referred specimens.—USNM 22415 (from Knight Member). CU 42823, 44703, 44718, 44839, 44844, 45253, 45277, 45327, CM 38736 (from Lost Cabin Member). Possibly AMNH 48165–48167, 48169, 48170 (from Almagre Member).

Emended diagnosis.—Smaller than *K. depressus* and larger than *K. minor*; anterior cingulum on the

Table 12.—*Dental measurements of* Knightomys senior *(in millimters).*

Specimen nos.	M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
CU 45277	1.70	1.31	1.55						
CU 45253	1.74	1.39	1.51						
CM 38736				1.65	1.55	1.66	1.93	1.57	1.55
CU 42823							1.95	1.66	1.59
	M^1			M^2			M^3		
CU 45327	1.54	1.54	1.48						
CU 44703				1.61	1.60	1.55			
CU 44844							1.69	1.72	—

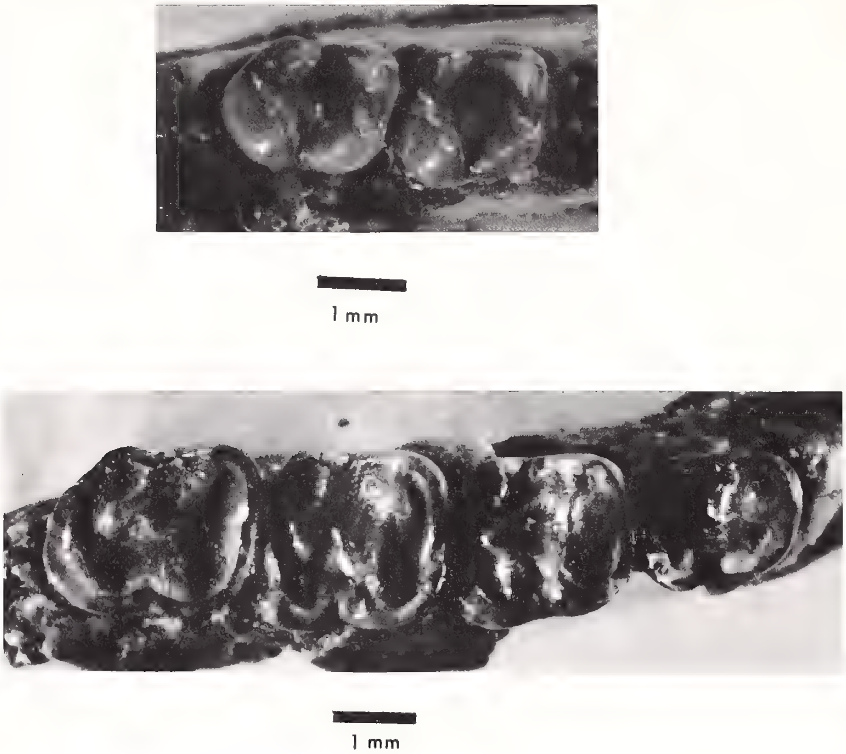


Fig. 27.—Lower dentitions of *Knightomys senior* and *K. huerfanensis*. A) *K. senior*, RM_2–M_3, CM 38736. B) *K. huerfanensis*, RP_4–M_3, AMNH 55114, holotype.

lower molars connected to protoconid; mesoconid on M_2–M_3 less elongated; hypolophid on lower molars short.

Discussion.—Gazin's (1952, 1961, 1962) hypodigm of *Knightomys senior* consisted of three mandibles, all with very heavily worn cheek teeth. Several specimens from San Jose Formation are questionably referable to this species. The specimens from New Mexico are slightly smaller than *K. senior* and slightly larger than *K. minor*. The specimens of *K. senior* from the Lost Cabin Member of the Wind River Formation are equivalent in size to the typotypic material of *K. senior* and are less worn, thus helping to define the species.

Wood (1965) separated *K. senior* from *K. depressus* on only a few distinctions: 1) single mental foramen in *K. senior*, double in *K. depressus*; 2) hypolophid on the molars of *K. senior* is directed toward the hypoconulid; 3) sides of I_1 of *K. depressus* are more nearly parallel; and 4) *K. senior* is smaller.

The first distinction, a single mental foramen on *K. senior*, is incorrect. The type of *K. senior* and all referred specimens of the species have a minute second mental foramen as in all other *Knightomys* (see Gazin, 1962: Pl. 5, Fig. 6). The second difference, the direction of the hypolophid, is variable in *K. depressus* and could not be determined from the specimens in Gazin's (1962) hypodigm. The new material of *K. senior* shows that the hypolophid on the molars is very short and less variable in length and direction than in *K. depressus*. There is no real distinction between the lower incisors of *K. depressus* and *K. senior* except for size.

In all, size is the only difference between *K. depressus* and the original hypodigm of *K. senior*. The specimens from the Lost Cabin Member of the Wind River Formation preserve better the occlusal morphology of the cheek teeth of *K. senior*. These specimens differ from *K. depressus* in having: 1) a thin anterior cingulum connecting with the protocone as in *K. minor*; 2) an entoconid with a shorter hypolophid; and 3) a smaller mesoconid that does not extend as far into the talonid basin. These differences, along with smaller size, distinguish *K. senior* from *K. depressus*. *Knightomys senior* is larger than *K. minor*, and does not possess the central cuspule on the anterior cingulum of M_1 of *K. minor*.

The single specimen from the Cathedral Bluffs

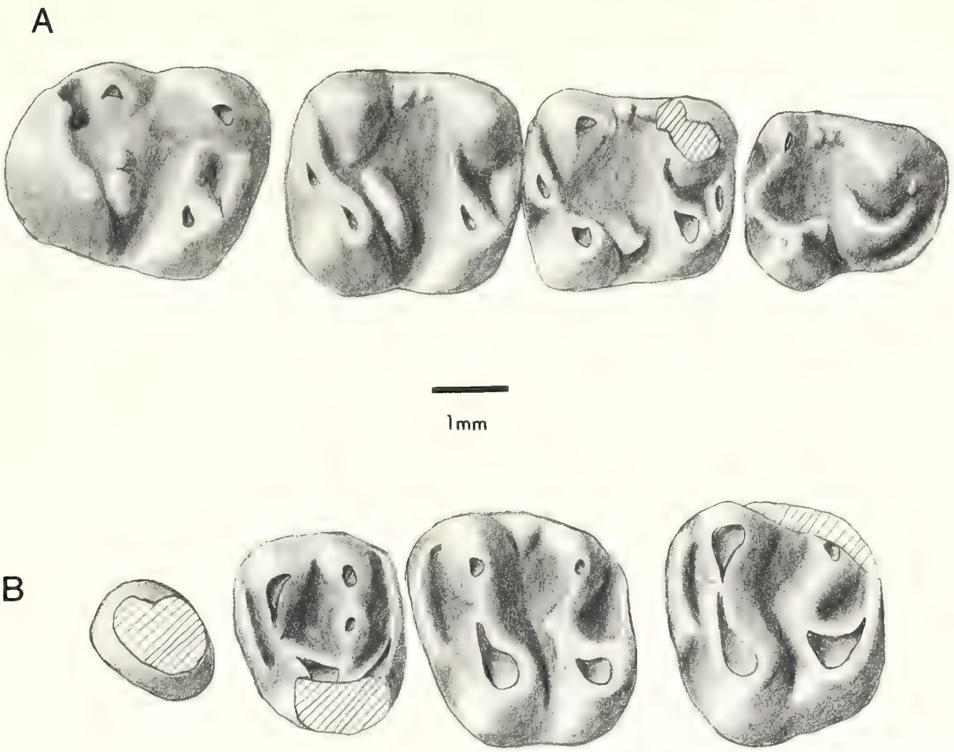


Fig. 28.—Cheek teeth of *Knightomys huerfanensis.* A) RP_4–M_3, AMNH 56523. B) LP^3–M^2, CU 26233.

Tongue of the Wasatch Formation allocated by West (1973) to *Knightomys* cr. *K. senior* is here referred to *K. depressus.*

Knightomys huerfanensis (Wood, 1962)
(Figs. 27, 28, Table 13)

Paramys huerfanensis Wood, 1962.
Microparamys sp. B Wood, 1962.
Knightomys sp. West, 1973.

Type specimen.—AMNH 55114, right mandible with worn P_4–M_3.

Horizon and locality.—Type and some referred specimens from localities II, III, V, upper Huerfano Formation, Colorado. Other referred specimens from Cathedral Bluffs Tongue, Wasatch Formation, Colorado; and Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late to latest early Eocene (Lostcabinian to Gardnerbuttean).

Referred specimens.—AMNH 17025, 17462, 55115, 55119, 55131, 55136, 55140, 55191, 55200, 55989, 56523, YPM 16438, 16480, CM 19537, CU 22040, 26233, 29944, 32753, 32786, 33267, 33272 (from Upper Huerfano, localities II, III, V). FMNH PM 15524, PM 15587, PM 15889 (from the Cathedral Bluffs Tongue). CM 37175, CU 42852, 42854, 44723, 45224, 45420 (from Lost Cabin Member).

Emended diagnosis.—Largest species of genus; cusps on cheek teeth large and rounded; hypolophid on lower molars short; lophs on molars relatively high; metaloph and protoloph on P^4 nearly parallel; anterior cingulum separated from protoconid and metaconid on lower molars.

Description.—*Knightomys huerfanensis* is distinctly larger than any other species of *Knightomys.* The skull and mandible of *K. huerfanensis* strongly resemble those of *K. depressus* but are larger and more robust. Little else can be determined from the skull material of *K. huerfanensis* because of its poor condition (CU 29944).

The cusps on the cheek teeth of *K. huerfanensis* are large and high. The lophs on the cheek teeth are also higher than in any other species of *Knightomys.*

P^4 has a relatively large hypocone. The metaloph and protoloph converge at the protocone but are more nearly parallel than in other species. There is no protoconule but the metaconule is distinct.

The upper molars differ from those of other species only in having higher, more rotund cusps. In other species of *Knightomys,* the protocone and hypocone of M^1–M^2 are more cresentic. In *K. huerfanensis,* these cusps are more nearly circular. The upper incisors of *K. huerfanensis* differ from those of *K. depressus* only in being larger.

As in the upper molars, the lower cheek teeth of *K. huerfanensis* are distinct from other species in having higher cusps and lophs. The anterior cingulum on the molars is reduced to a globular

Table 13.—*Dental measurements of* Knightomys huerfanensis *(in millimeters).*

Specimen nos.	P_4			M_1			M_2			M_3		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
AMNH 55989	—	—	—	2.10	1.79	1.95	—	—	—	—	—	—
AMNH 17462	—	—	—	—	—	2.09	2.23	1.97	2.18	2.55	2.05	2.1
YPM 16480	—	—	—	—	—	—	—	—	—	2.25	1.99	1.6
AMNH 55119 L	2.06	1.66	1.79	2.17	1.88	2.08	2.40	2.12	2.09	—	—	—
AMNH 55119 R	2.13	1.53	1.74	2.10	1.88	2.04	2.36	2.04	1.99	2.73	2.09	2.0
AMNH 55191	2.07	1.52	1.78	2.16	—	—	2.25	2.14	2.35	2.56	2.10	2.1
AMNH 55136	2.04	1.47	1.73	2.07	1.75	1.89	2.12	1.98	2.07	—	—	—
AMNH 55131	—	—	—	—	—	—	2.19	2.05	2.10	2.47	1.96	2.0
AMNH 55140	—	—	—	2.06	1.64	1.89	2.15	1.88	2.10	—	—	—
AMNH 56523	2.00	1.53	1.74	2.14	1.79	1.97	2.20	2.11	2.08	2.50	2.00	1.8
CU 32753	1.86	1.38	1.62	2.12	1.69	1.85	2.23	1.86	2.02	2.32	1.87	1.9
CU 29944	—	—	—	2.02	—	1.98	—	—	—	—	—	—
		P^4			M^1			M^2			M^3	
CU 26233 L	1.73	1.98	2.06	2.17	2.34	2.23	2.14	2.46	2.21	—	—	
CU 26233 R	—	—	—	—	—	—	2.11	2.51	2.19	1.96	2.27	
CU 32786	1.92	2.20	2.04	—	—	—	—	—	—	—	—	
CU 19537	1.64	2.09	1.98	—	—	—	—	—	—	—	—	
CU 22040	—	—	—	—	—	—	2.08	2.22	2.07	2.13	2.17	
CU 33267	—	—	—	2.21	2.44	2.25	—	—	—	—	—	
CU 33272	1.87	2.23	2.10	—	—	—	—	—	—	—	—	

swelling along the anterior margin of the tooth. It is not connected to any cusp. The metastylid on all the lower cheek teeth is larger and more distinct than in any other species of the genus. The hypolophid on the lower molars is short and directed buccally. It is shorter than in many specimens of *K. depressus* or *K. minor,* but is high and persists until late stages of wear.

The lower incisor of *K. huerfanensis* is narrow and parallel sided, resembling that of all other species of the genus. The anterior surface of I_1 is either flattened or convex.

Discussion.—The holotype of *Knightomys huerfanensis* (AMNH 55114) is a mandible with heavily worn cheek teeth. Because the occlusal pattern of the cheek teeth of the type is so badly obscured, Wood (1962) could not distinguish any of the sciuravid characters of the species, and referred it to *Paramys.* Additional unworn specimens from the Huerfano, the type area of the species, indicate that this species is readily assignable to *Knightomys. Knightomys huerfanensis* differs from *K. depressus* only in its larger size and more robust cusps and lophs on the cheek teeth.

Wood (1962) identified a single specimen from the Huerfano as an upper molar of *Microparamys* sp. B (AMNH 55200). This tooth agrees in size and morphology with P^4 of *K. huerfanensis.*

Three isolated molars from the Cathedral Bluffs, originally identified as *Knightomys* sp. (West, 1973), are also referable to *K. huerfanensis.*

Pauromys Troxell, 1923

Type species.—*Pauromys perditus* Troxell, 1923.

Pauromys sp.
(Fig. 29, Table 14)

Referred specimens.—CU 44710, 44711, 44713, 44734, 44842, 45258, 45259, 45270, 45292.

Horizon and locality.—Deadman Butte area (Stucky and Krishtalka, 1982), Lost Cabin Member, Wind River Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Description.—The upper molars are square in outline. The protoloph and metaloph are distinct buccolingually directed lophs. The anterior cingulum runs parallel to the protoloph from the buccal margin of the tooth to the level of the apex of the protocone. The posterior cingulum arises from the hypocone and runs the entire width of the tooth. No protoconule is present. A minute anterior projection originates at the metaconule and runs about half the width of the valley separating the protoloph and metaloph. A second minor loph originates from the protocone and runs posterobuccally toward the metaconule spur but does not connect with it on unworn specimens. A minute mesostyle is present. A single dP^4 (CU 44373), near the size of the upper molars of *Pauromys* sp., may represent this species. This tooth is triangular in occlusal outline, the hypocone is posterobuccal to the protocone and separated from the protoconid. The posterior cingulum, originating at the hypocone, runs the width of the tooth. The protocone is connected to the buccal cusps (paracone and metacone) by the protoloph and metaloph which converge on the protocone.

P_4 is quite small and triangular in shape. The metaconid dominates the trigonid with a small, closely appressed protoconid. The mesoconid is minute and isolated. The entoconid and hypoconid are connected by a continuous posterolophid.

M_1 is narrower anteriorly than posteriorly. The anterior cin-

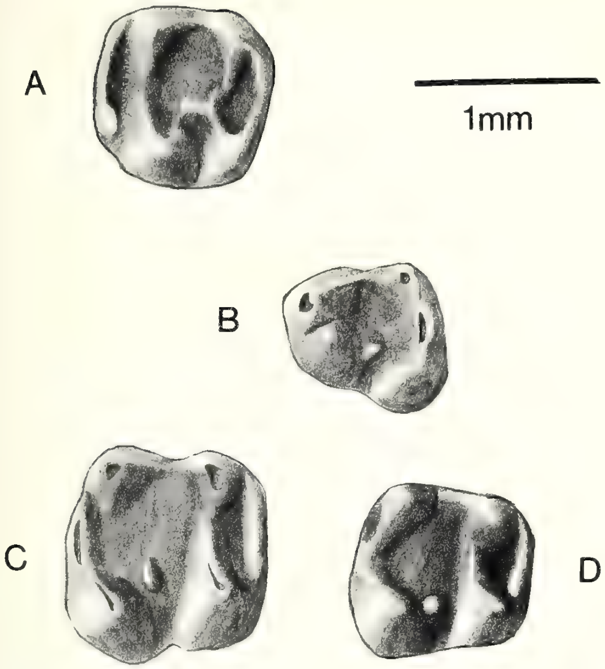


Fig. 29.—Cheek teeth of *Pauromys* sp. A) LM^1 or M^2, CU 44710. B) LP_4, CU 45270. C) RM_2, CU 45292. D) RM_1, CU 44713.

gulum is short but extends anterior of the protoconid and metaconid, not continuous with either cusp. The posterior arm of the protoconid is relatively long, ending lingually at the posterobuccal corner of the metaconid. A small, low ridge from the metaconid enters the trigonid basin. A metastylid is present on the posterolingual slope of the metaconid. The mesoconid, as in P_4, is minute and isolated. The hypoconid is connected to the entoconid by way of the posterolophid which flexes at its center.

M_2 is nearly square in outline. The anterior cingulum and posterior arm of the protoconid are arranged as in M_1. The mesoconid is isolated but extends lingually into the talonid basin. The hypoconid is continuous with the posteroloph but separated from the entoconid. A low partial hypolophid runs buccally from the entoconid.

Discussion.—All specimens of *Pauromys* sp. from the Lost Cabin Member are isolated teeth. The molars assigned to this species are equal in size to the molars of *Pauromys perditus* and *Pauromys* sp. from the Bridgerian (Troxell, 1923; Dawson, 1968*b*). The P_4 of the Lost Cabin species is larger than any P_4 of the Bridgerian species. This condition would be predicted in the earlier species if reduction of the lower premolar is occurring in this genus through time.

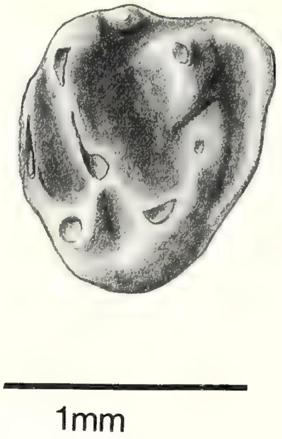


Fig. 30.—Upper cheek tooth of an indeterminate sciuravid, AMNH 59632.

The molars of the Lost Cabin species have lower lophs than the Bridgerian species but have little else that separates them from the later species. Dawson (1968*b*) noted that the minute loph from the metaconule and protocone on the upper molars of Bridgerian *Pauromys* sp. were connected on some specimens but that this was a variable character. These two small lophs never meet on the upper molars of the Lost Cabin species except when they are extremely worn.

The material of *Pauromys* sp. from the Lost Cabin Member is too scanty and too similar to the Bridgerian species of *Pauromys* to establish a new species, but does confirm the trend in the reduction of P_4 and the increase in the height of the lophs in this genus through time.

?Sciuravid indeterminate
(Fig. 30)

Specimen.—AMNH 59632, isolated upper cheek tooth.

Horizon and locality.—East Alheit Pocket Quarry (McKenna, 1960), Wasatch Formation, Colorado.

Age.—Early early Eocene (Graybullian).

Description.—AMNH 59632 is a minute tooth (a–p = 1.02 mm, tra = 1.04 mm). It is approximately triangular in outline. The anterior cingulum is widely separated from the paracone but converges with the protoloph at the level of the apex of the protocone. Protoloph and metaloph converge at the protocone. Both conules are relatively large. The protoloph is not continuous between the paracone and the protoconule. The metacone is anteroposteriorly compressed and smaller than the paracone. A mesostyle is present. A hypocone nearly equal in size to the protocone is posterior and lingual to the protocone. A short loph connects it with the metaconule. The posterior cingulum originates at the hypocone and runs buccally to the level of the metacone.

Discussion.—AMNH 59632 is referred to the Sciuravidae because of the large hypocone and degree

Table 14.—*Dental measurements of* Pauromys *sp. (in millimeters).*

Measurements	CU 45270	CU 44713	CU 45292	CU 44842	CU 44710	CU 45259	CU 44711	CU 45258
P_4 a–p	0.81							
tra	0.59							
trp	0.73							
M_1 a–p		0.95						
tra		0.74						
trp		0.82						
M_2 a–p			1.07					
tra			0.97					
trp			1.06					
M^1 a–p				0.98	0.95	1.04	1.13	1.00
or tra				1.08	0.94	1.08	1.13	0.96
M^2 trp				0.96	0.91	—	0.96	0.89

of loph development. It is difficult to determine exactly which tooth this specimen is. It would be difficult to call AMNH 59632 a P^4 because of its marked molariformity. However, dP^4 in most ischyromyids has a hypocone that is relatively large and lingual to the protocone and a triangular shape.

The only sciuravid or ischyromyid known from the Four Mile fauna near the size of AMNH 56932 is *Apatosciuravus bifax.* AMNH 56932 may represent a dP^4 of this species but appears too small even for *A. bifax.* The occurrence of AMNH 59632 is important because if it represents a distinct species of sciuravid, it would represent the earliest occurrence of this family.

Family ?Cylindrodontidae Miller and Gidley, 1918

Dawsonomys Gazin, 1961

Type species.—*Dawsonomys woodi* Gazin, 1961.

Dawsonomys woodi Gazin, 1961

(Fig. 31)

Type specimen.—USNM 19309, left mandible with P_4–M_1.

Horizon and locality.—LaBarge (Gazin, 1952:6), Knight Member, Wasatch Formation, Wyoming.

Age.—Late early Eocene (Lostcabinian).

Discussion.—Gazin (1961) erected *Dawsonomys woodi* based on a mandible with I_1 and P_4–M_1. He referred this genus to the Sciuravidae because of the level of development of the lophs on the cheek teeth.

Later, Wood (1965) named a second species, *D. minor,* from the Lysite Member, Wind River Formation. As mentioned above, new material of *D. minor* indicates that this species is referable to *Knightomys,* leaving only the type species in *Dawsonomys.*

No new material of *D. woodi* has been collected since Gazin's (1961, 1962) original description of the type specimen. *Dawsonomys* is here referred questionably to the Cylindrodontidae based on its similarity to the Bridgerian cylindrodontid *Mysops.* I_1 of *D. woodi* is rounded anteriorly and laterally and much broader than in sciuravids, but typical for *Mysops* and later cylindrodontids. I_1 of *D. woodi* more closely approaches that of later cylindrodontids than does that of *Mysops.* M_1 of *D. woodi* has features that agree with *Mysops* and other cylindrodontids as well: 1) anteroposteriorly compressed and elevated trigonid; 2) entoconid more anterior with a deep valley between it and the posterolophid; 3) minute mesoconid; 4) ectolophid joins hypoconid but not protoconid; and 5) a complete hypolophid.

P_4 of *D. woodi* is submolariform and has many of the features of M_1 such as a partial hypolophid and weak ectolophid. It is nearly equal in size to M_1. In *Mysops,* P_4 is reduced in size and complexity, unlike that of *Dawsonomys.*

Both P_4 and M_1 of *D. woodi* are more rectangular in outline than in *Mysops.* In all observable features, *Dawsonomys* represents a very primitive cylindrodontid. Its definite inclusion in the Cylindrodontidae should be based on additional material, especially upper cheek teeth. Based on the presently known material, *Dawsonomys* is best placed in the Cylindrodontidae, thus extending the range of the family into the early Eocene.

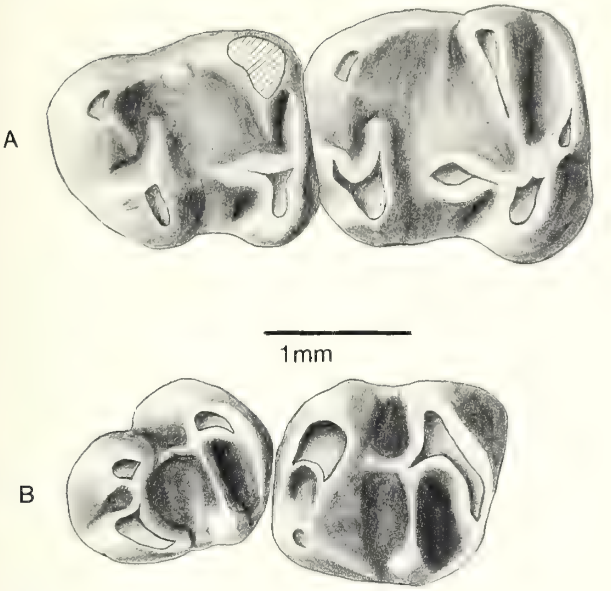


Fig. 31.—P_4–M_1 of *Dawsonomys* and *Mysops*. A) *Dawsonomys woodi*, LP_4–M_1, USNM 19309, holotype. B) *Mysops parvus*, RP_4–M_1, USNM 17663.

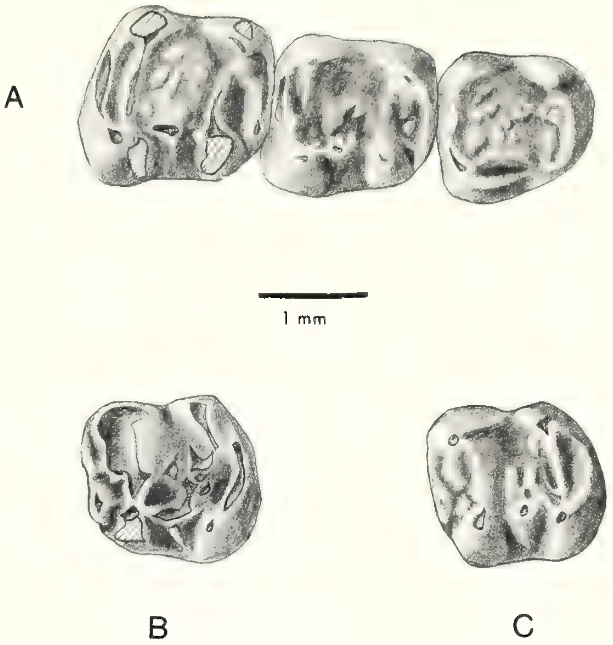


Fig. 32.—Lower cheek teeth of *Mattimys kalicola*. A) RP_4–M_2, AMNH 14731, holotype. B) LM_1, CM 36527. C) LM_2, CM 36526.

Family ?Eutypomyidae Miller and Gidley, 1918

Mattimys, new genus

Type species.—*Mattimys kalicola* (Matthew, 1918).

Range.—Early Eocene of Wyoming.

Emended diagnosis.—Very small rodent; lower cheek teeth increase in size from P_4–M_2; broad, low swellings present in talonid basin of all lower cheek teeth; mesoconids on lower molars large but ectolophids lacking; posterior arm of protoconid runs the entire width of molars, joining metaconid; anterior cingulum on molars runs entire width of tooth, extending lingually anterior to metaconid and terminating buccally as a cuspule anterior to protoconid; metaconid equal to entoconid in size; hypolophid originates from entoconid on M_1–M_2 and unites with center of posterolophid on M_1 and with hypoconid on M_2.

Etymology.—Patronym for W. D. Matthew, who first described *Mysops kalicola*.

Mattimys kalicola (Matthew, 1918)
(Fig. 32, Table 15)

Mysops kalicola Matthew 1918.
"*Mysops*" *kalicola* Matthew, Wilson, 1937.

Type specimen.—AMNH 14731, right mandible with P_4–M_2.

Table 15.—*Dental measurements of* Mattimys kalicola *(in millimeters).*

Specimen nos.	P_4			M_1			M_2		
	a–p	tra	trp	a–p	tra	trp	a–p	tra	trp
AMNH 14731	1.35	1.12	1.35	1.46	1.26	1.44	1.59	1.48	1.53
CM 22242				1.42	1.32	1.43			
CM 36523				1.45	1.36	1.39			
CM 22243				1.44	1.33	1.44			
CM 35863				1.44	1.42	1.46			
CM 36527				1.49	1.21	1.38			
CU 44365				1.49	1.24	1.36			
CM 36526							1.37	1.29	1.30
CU 44836							1.42	1.38	1.44

Horizon and locality.—Type from type area of the Lost Cabin Member, Wind River Formation, Wyoming, and all referred specimens also from the Lost Cabin Member, Wind River Formation.

Age.—Late early Eocene (Lostcabinian).

Referred specimens.—AMNH 14730, CM 22242, 22243, 35863, 36523, 36526, 36527, CU 44365, 44714, 44836, 45352.

Emended diagnosis.—As for genus.

Description.—The upper cheek teeth of *Mattimys kalicola* are not known. The mandible is shallow. The masseteric fossa on the mandible ends anteriorly below the anterior end of M_2. A single mental foramen is present on the mandible, level with the middle of the diastema anteriorly, and placed relatively high.

All of the lower cheek teeth have shallow talonid basins filled with small, randomly placed swellings that persist throughout all stages of wear. P_4 is the smallest tooth. It is rounded anteriorly. The metaconid is the largest cusp on P_4 but is not much higher than the entoconid or hypoconid. There is no mesoconid, but a low ectolophid connects the entoconid and hypoconid. There is a distinct hypoconulid at the center of the posterolophid. The anterior cingulum on M_1–M_3 runs the entire width of the tooth. It arises lingually from the anterolingual slope of the metaconid and runs anterior to the metaconid. It terminates as a small cuspule buccally anterior to the protoconid. The posterior arm of the protoconid on the molars is a relatively high loph which runs straight lingually and joins the metaconid at its base. An accessory loph runs into the trigonid basin from the metaconid and ends at the center of the basin. Another short loph into the trigonid basin from the protoconid is variably present. There is no ectolophid on the lower molars. The mesoconid is relatively large and generally has a minor loph running into the talonid basin. The posterolophid is continuous between hypoconid and entoconid. The metaconid is nearly equal in size to the entoconid, unlike early ischyromyids where the metaconid is always higher. There is no trace of a metastylid on any of the cheek teeth.

M_1 is smaller than M_2. A hypolophid runs from the entoconid on M_1 buccally and merges with the center of the posterolophid. On M_2 the hypolophid runs the entire width of the tooth and joins the hypoconid. M_3 is rounded posteriorly and lacks a hypolophid. In all other features, M_3 resembles M_1 and M_2.

The lower incisor is rounded anteriorly. The cross-sectional shape of I_1 is roughly tear-drop shaped, relatively broad anteriorly and tapering to a point posteriorly. Enamel extends only slightly onto the medial and lateral sides of the incisor.

Discussion.—In his original description, Matthew (1918:618) provisionally referred this species to *Mysops,* an otherwise Bridgerian genus. He listed the type (AMNH 14731) and two referred specimens from the type area of the Lost Cabin Member of the Wind River Formation. Wilson (1937) pointed out that one of the referred specimens (AMNH 14729) did not belong to the same species as the type. Later, Dawson (1966) referred AMNH 14729 to *Microparamys lysitensis* which was later synonymized with *Knightomys depressus* (Guthrie, 1971). Several additional specimens, including those referred by Guthrie (1971) to "sciuravid cf. *Dawsonomys minor,*" have been recovered since Matthew's description.

Wilson (1937, 1949) considered "*Mysops*" *kalicola* a paramyine, and included it in his "*Paramys*" *buccatus* species group. Wood (1962) failed to discuss "*Mysops*" *kalicola* in his review of the Paramyidae because he did not consider it a paramyid. Dawson (1966:105) pointed out many similarities between "*Mysops*" *kalicola* and the Uintan species *Janimus rhinophilus* which, in turn, shared many similarities with early Oligocene *Eutypomys* from Texas. Black (1971) placed *Janimus* in the Reithroparamyinae in the Ischyromyidae but did not include "*Mysops*" *kalicola* in his classification. Guthrie (1971) included *Mysops kalicola* (without question marks) in the Sciuravidae without discussion.

Wood (1974) described a new primitive species of *Eutypomys, E. inexpectatus,* from the earliest Oligocene of Texas and compared it with *Janimus.* He included *Janimus* in the Microparamyinae (of the Paramyidae) rather than in the Eutypomyidae because of possible differences in the zygomasseteric structure but suggested that *Janimus* might represent a "collateral ancestor" (Wood, 1974:96). Later Dawson (1977:198) placed *Janimus* in "Family uncertain," stating ". . . this genus may be an early representative of the Eutypomyidae."

An undescribed isolated lower molar from the Duchesnian locality 20, Badwater Creek area, Wyoming (see Black and Dawson, 1966, for locality and age) is intermediate between *Janimus* and *E. inexpectatus* in size and morphology. This specimen supports the idea of a close relationship between *Janimus* and *Eutypomys.*

Mattimys kalicola has a number of similarities with *Janimus* (Dawson, 1966:105–106). The differences between *Mattimys* and *Janimus* are mostly primitive features in *Mattimys.* The hypolophid on M_2 of *Mattimys* runs the entire width of the tooth. In *Janimus* the hypolophid joins the posterolophid at its center. This may be the only feature in which *Mattimys* is more advanced than *Janimus.*

A single M^3 from the Bridger Formation (FMNH PM 15193), identified as *Microparamys* sp. B by West (1973), is comparable in size to *J. rhinophilus.* It has a number of prominent wrinkles in its central basin. These wrinkles are similar to those of the teeth of *Mattimys* and are not fine crenulations as in species of *Lophiparamys* and *Thisbemys.* This tooth probably belongs to either *Mattimys* or *Jan-*

imus, or represents an intermediate form between these two genera.

Because of possible differences in the zygomasseteric structure of *Janimus,* Wood (1974) suggested that it may represent an entirely different suborder, as well as family, from *Eutypomys.* The zygomasseteric structure of *Mattimys* is unknown but the position of the masseteric scar on the mandible does not differ from that of early ischyromyids, suggesting that no modification in the masseteric structure has occurred. Therefore, if *Mattimys* were included in the Eutypomyidae, the family would have members with both protrogomorphous and sciuromorphous zygomasseteric structures. This would also mean that sciuromorphy in this lineage was developed independently from other sciuromorphs. This is not a unique situation. Early sciurids (Black, 1963) do not have a completely sciuromorphous structure, but are clearly referable to the same family as the later fully sciuromorphous sciurids.

The union of *Mattimys, Janimus* and *Eutypomys* is based on the very strong similarity of their dentitions. Thus, both *Janimus* and *Mattimys* are here considered eutypomyids.

Two specimens from the Graybullian Four Mile fauna, an M_3 (UCMP 44103) and M_2 (UCMP 44104) were identified by McKenna (1960:84) as "?Subfamily Paramyinae, undescribed genus and species." He noted the similarity between these specimens and *Mattimys kalicola* but stated that there were significant differences, though he did not list them. The present location of these specimens is unknown (D. Savage and D. Guthrie, personal communication) but according to McKenna's (1960: Figs. 42a, b) figures, these specimens are very similar to M_2–M_3 of *Mattimys kalicola.* M_2 from the Four Mile fauna differs from that of *M. kalicola* in having wider trigonid than talonid, the metaconid obliquely compressed, and a less distinct hypolophid. In all other features this specimen is identical to M_2 of *M. kalicola.* The posterolophid of the Four Mile M_3 is not as strong as that of M_3 of *M. kalicola.* These specimens from the Four Mile fauna should be referred to *Mattimys,* without a specific identification.

CONCLUSIONS

Primitive Cranial and Dental Morphologies of Rodents

In the past, the origin of the rodents was believed to be found in Paleocene primates (Wood, 1962) or primitive "insectivores" (see Szalay, 1977:355–356). More recent discoveries of Paleocene mammals from the People's Republic of China have produced eurymyloids that show many resemblances to rodents, notably the late Paleocene eurymyloid *Heomys* (Li, 1977). These similarities led Hartenberger (1980) to suggest the origin of rodents from the Eurymyloidea (Li, 1977; =Mixodontia, Sych, 1971). Early Eocene ctenodactyloids from Asia such as "*Microparamys*" *lingchaensis* (Li et al., 1979) and *Tamquammys* (Shevyreva, 1971) share many dental features with *Heomys* (Dawson et al., in press) and support the idea of an Asian origin of rodents from a eurymyloid stock.

Traditionally, primitive ischyromyids (="paramyids" or "paramyines") have been viewed as the most primitive rodents that gave rise to all later rodents (for example, Wilson, 1949; Wood, 1962). However, with the recent evidence of early eurymyloids and ctenodactyloids from Asia, it appears that perhaps ctenodactyloids may represent the most primitive rodents (Dawson et al., in press) and the ischyromyids represent only the basal stock for certain later rodent groups.

Some of the dental fearures of *Heomys* that are also present in early ctenodactyloids (Dawson et al., in press) are: P^4 with single buccal cusp (paracone) and small, distinct hypocone; upper molars with well developed hypocone and metaloph directed anterolingually forming a "V" with the protoloph; P_4 with minute talonid; lower molars with large hypoconulid. All of these features are here considered primitive for rodents.

If the ctenodactyloids do indeed represent the primitive condition, the ischyromyids that are the most primitive are the reithroparamyines, which maintain a hypocone on P^4 and a distinct hypoconulid on the lower molars. The hypocones on the upper molars are relatively larger than in paramyines in reithroparamyines as well. The simpler pattern of the molars in paramyines would be more derived. *Reithroparamys ctenodactylops* maintains more primitive ctenodactyloid features than any other ischyromyid.

Wood (1962) viewed *Franimys amherstensis* from the Clarkforkian of the Bighorn Basin as the most primitive rodent. He believed that the primary buccal cusp on P^4 was the metacone and the paracone developed secondarily. This theory was based on a misinterpretation of the type specimen of *F. amherstensis* and does not seem likely in view of the recent discoveries of early ctenodactyloids from Asia.

Features of the skull and mandible that are considered to be primitive are: 1) nasal bones extend posteriorly to a level even with the posterior margin of the premaxillaries; 2) double mental foramen on the mandible; 3) posterior margin of the anterior root of the zygoma even with the posterior margin of P^4; 4) auditory bulla not ossified to the skull.

All reithroparamyines, pseudoparamyines, sciuravids, and early ctenodactyloids have the first feature listed above. The extent of the nasals and premaxillaries in *Heomys* is not known, but in several other eurymyloids the premaxillaries extend farther posteriorly than the nasals. In the Paramyinae, the nasals extend farther posteriorly than the premaxillaries, an obviously derived condition.

A double mental foramen on the mandible is present in *Heomys* and nearly all early ischyromyids and sciuravids. There is independent reduction to a single foramen several times.

The posterior margin of the anterior root of the zygoma in primitive mammals (such as insectivores, primates, and carnivores) is level with the posterior molars, and may even be farther posterior than M^3. In *Heomys,* it is level with the posterior margin of M^1. This continued forward movement of the zygoma is also present in rodents. The posterior margin of the anterior root of the zygoma in early ctenodactyloids and most paramyines is level with the posterior margin of P^4. In reithroparamyines it progressively moves forward until it is level with the anterior margin of P^4 in *Microparamys* and *Apatosciuravus.*

The anterior movement of the zygoma is accomplished independently in many lineages. In manitshines it moves forward, but not to the extent that it does in *Microparamys.* In two genera, *Mytonomys* and *Quadratomus,* the zygoma is more posterior. This is viewed as posterior movement from the primitive condition because these genera are otherwise quite derived and this feature is not present in any other members of their subfamilies of the Ischyromyidae.

It is consistent with nearly all other orders of early Tertiary mammals to suggest that the lack of a bony auditory bulla coossified with the skull is primitive for rodents. However, evidence from early species of rodents is rare and inconclusive. All Eocene ischyromyids except *Reithroparamys* (including "*Paramys*" *sciuroides*), for which basicranial material is preserved, lack a bulla ossified to the skull. Wood (1962) demonstrated that in some paramyines there is evidence that there was a bony bulla, but that it was not coossified with the skull. The earliest ctenodactyloid from Asia is known to preserve an ossified bulla at least loosely attached to the skull (Li, personal communication). All skulls of eurymyloids available to the author for study have bony auditory bullae ossified to the skull. The lack of a bony bulla coossified to the skull in rodents is here considered to be the primitive condition because of lack of any evidence to the contrary and the very poor evidence of the basicaraial region of early rodents.

Relationships of North American Paleocene and Early Eocene Rodents

Ischyromyidae

As stated above, the reithroparamyines represent the most primitive ischyromyids. The features that unite the reithroparamyines are the anterior position of the zygoma and masseter on the mandible and certain dental characters (discussed above). All paramyines can be derived from a primitive reithroparamyine stock by lengthening of the nasal bones of the skull and simplification of the occlusal pattern of the cheek teeth (Fig. 33). The most primitive paramyine is *Paramys taurus,* which possesses some of the primitive reithroparamyine characters, such as a hypoconulid on the lower molars and hypocone on P^4. These features are, however, reduced in *P. taurus* and continue to be more greatly reduced in later paramyines. The presence of an attached auditory bulla in reithroparamyines is considered an advanced character that might bar the Reithroparamyinae from ancestry of paramyines. However, this character is only known in middle and late Eocene species of reithroparamyines. Earliest species of reithroparamyines may not have possessed this character, and it was not developed in the Reithroparamyinae until after the Paramyinae had already split off.

Pseudoparamyines have an even simpler P^4 in their earliest forms, and can be readily derived from a paramyine stock.

The Paramyinae are well diversified in the late Eocene and a few genera persist into the early Oligocene (see Black, 1971; Wood, 1962, 1974; Storer, 1978). Wood (1962) and Black (1963) believed that the sciurids, which first appear in North America in the Oligocene, were possibly derived from the late Eocene paramyine *Uriscus.* This theory appears consistent with the trend in paramyines toward a simplification of the occlusal pattern of the dentition. It is also consistent with the derived features

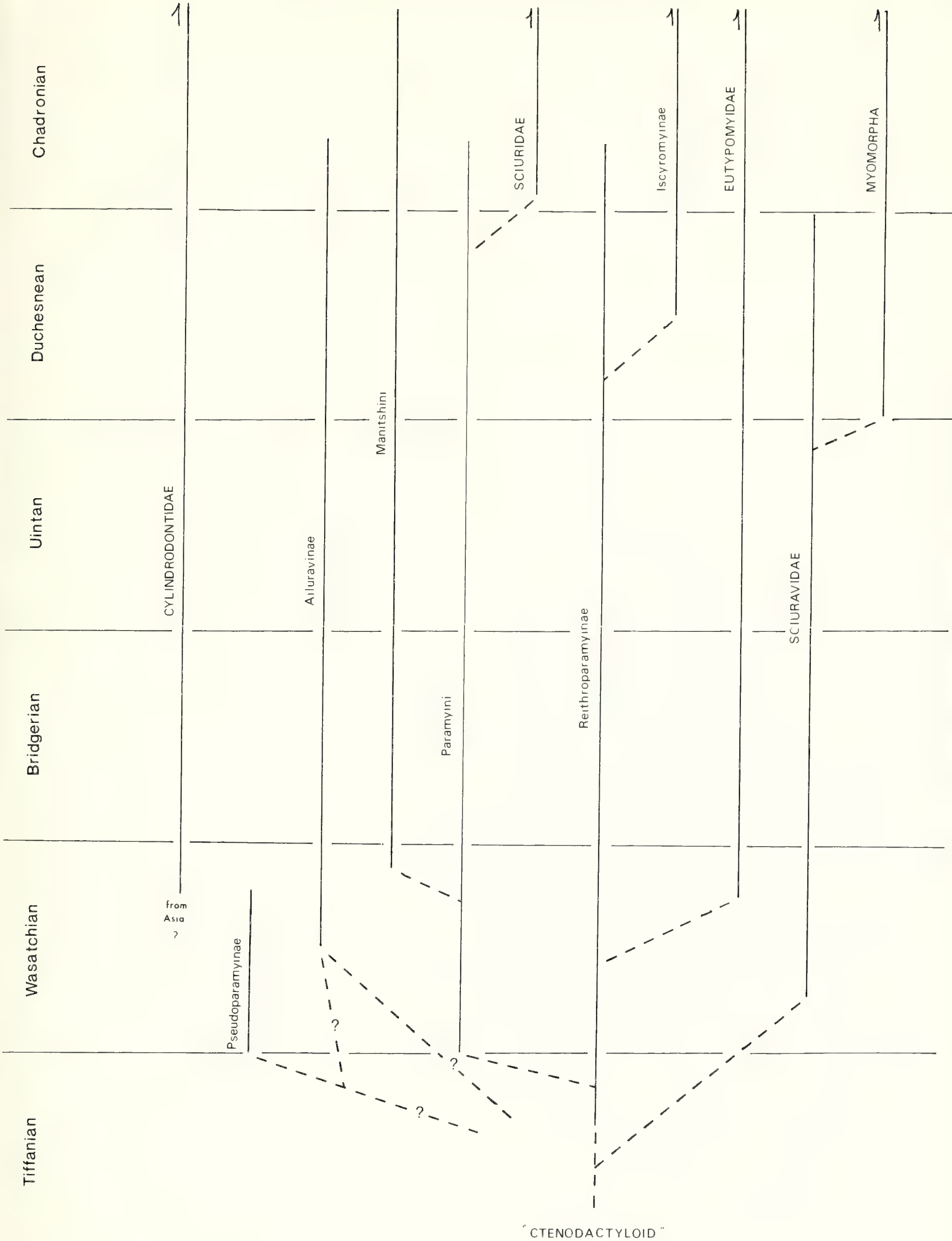


Fig. 33.—Proposed relationships of Eocene rodents in North America.

of the skulls of paramyines. The earliest sciurids have nasals that extend farther posterior than the premaxillaries (Black, 1963).

In several papers, both Wood (1962, 1976*a*) and Black (1968*a*, 1971) derived the Ischyromyinae (or Ischyromyidae) from the Paramyinae. The two genera that were suggested as possible ancestors to *Ischyromys* were *Leptotomus* and *Rapamys.* This phylogeny was based on dental characters. However, *Ischyromys* (including *Titanotheriomys* Matthew, 1910) maintains the primitive condition of its nasal bones which has been lost in paramyines. On this basis, ischyromyines cannot be derived from a paramyine.

Dentally, *Ischyromys* has a hypocone on P^4 and a relatively large hypocone on the upper molars. These too, do not follow the condition in *Leptotomus* or *Rapamys,* in which the upper dentition is simplified and the hypocones reduced or lost. Wahlert (1974) discounted the possibility of *Leptotomus* being an ancestor of *Ischyromys* on the basis of cranial foramina. The Eocene ischyromyid that is probably closest to representing an ancestral form for *Ischyromys* is *Reithroparamys.* The middle and late Eocene species of *Reithroparamys* develop lophs on their cheek teeth similar in arrangement to those of *Ischyromys.* P^4 of *Reithroparamys* is submolariform with a hypocone, also as in *Ischyromys.* Other features shared by these two genera are: 1) shorter, more tapered snout; 2) large bony auditory bulla fused to the skull; 3) anterior position of the anterior root of the zygoma; 4) masseteric fossa on the mandible marked by low ridges and terminating in a V-shape anteriorly; 5) double hypoglossal foramina; and 6) the presence of a post alar fissure on the skull. These features, and possibly the fusion of the scaphoid and lunar bones of the pes, relate these two genera. The dental pattern of *Ischyromys* can easily be derived from that of *Reithroparamys.* The only major difference between the Eocene *Reithroparamys* and the Oligocene *Ischyromys* is modification of the zygomasseteric structure of the skull. In all the features of the skull that differ, *Reithroparamys* represents the primitive condition from which the skull of *Ischyromys* can be derived.

Both Matthew (1910) and Wilson (1949) derived the Sciuravidae from what they termed the "*Paramys buccatus* group." This group (with the exception of *Franimys buccatus* itself) is very near the Reithroparamyinae as accepted here. Dawson (1968*b*, 1974) suggested that the origin of the sciuravids was to be found at or near the origin of *Microparamys.* Wood (1962: Fig. 90) derived the sciuravids from the *Microparamys* line, but also derived *Sciuravus* alone directly from *Paramys francesi.* Sciuravids are most easily derived from an *Apatosciuravus*-like ancestor (see discussion below).

Microparamys is the most likely ancestor for *Mattimys kalicola* and the eutypomyids. The most convincing evidence is from the morphology of the anterior cingulum on the lower molars, which is unique to *Microparamys* and its supposed relatives. Wood (1962: Fig. 90) derived "*Mysops*" *kalicola* from *Lophiparamys.* The teeth of both *Mattimys* and *Lophiparamys* are derivable from a basic *Microparamys* pattern, although the types of complications formed on the teeth of the first two genera are entirely different from one another along with other differences in dental morphology (Dawson, 1966).

The Pseudoparamyinae are represented by a single genus, *Franimys,* in North America and do not persist beyond the middle early Eocene. There are no probable descendants of *Franimys* later in the Eocene. The Ailuravinae, likewise, are represented by *Mytonomys* only. This genus however, persisted into the late Eocene (Wood, 1956, 1962; Black, 1968*b*) and earliest Oligocene (Wood, 1974). *Mytonomys* does not appear to be related to any later North American rodent except perhaps *Eohaplomys* from the late Eocene which has some similarities to the European *Ailuravus.*

Sciuravidae

The Sciuravidae are an exclusively North American family of rodents (see Dawson, 1977). It has been suggested that sciuravids originated directly from *Microparamys* (Wood, 1962) or somewhere near the origin of *Microparamys* (Dawson, 1968*b*, 1974). While some features of *Microparamys,* such as a large hypocone on the upper molars and anterior position of the zygoma, are shared with sciuravids, the unique morphology of the anterior cingulum of the lower molars of *Microparamys* is not present in the earliest known species of the primitive sciuravid, *Knightomys.* Thus, sciuravids cannot be directly derived from *Microparamys.* The hypocone on the upper molars of *Microparamys* is relatively larger than in other ischyromyids, but is not as large relatively as those of sciuravids. If it were accepted that all rodents are derived from a ctenodactyloid-like ancestor, a large hypocone is the primitive condition for rodents and the *Microparamys* condition is derived over that of the sciuravids.

The hypocone on the upper molars of *Apatosci-*

uravus is larger than that of any species of *Microparamys.* There is no feature of the upper dentition of *Apatosciuravus* that would bar it from an ancestral position to the sciuravids. P^4 of *Apatosciuravus bifax* has a weakly formed metaloph and no distinct metacone, which is an intermediate condition between P^4 of early ctenodactyloids and the earliest sciuravids or ischyromyids. However, the morphology of the lower molars of *A. bifax* cannot be interpreted in the same way. There is no indication of a hypolophid in *A. bifax,* and the buccolingual compression of the trigonids of M_1–M_2 is not present in sciuravids. If, however, *A. bifax* represents the most primitive sciuravid, the morphology of P^4 of this species would indicate a derivation of sciuravids from a ctenodactyloid ancestor separate from that of ischyromyids.

The earliest definite sciuravid is *Knightomys* from the early Eocene. The dental pattern of all Bridgerian and later sciuravids can be easily derived from that of *Knightomys.* Though the last sciuravids occur in the late Eocene, they have been long considered in the ancestry of later geomyoid and myomorph rodents (Wood, 1937; Wilson, 1949; Dawson, 1977).

Eutypomyidae

Mattimys kalicola is here believed to represent the earliest eutypomyid. It can be derived from *Microparamys* on the basis of dental morphology. Wood (1962) suggested that *M. kalicola* arose from *Lophiparamys.* However, *Lophiparamys* is already too specialized along its own line to have produced the molar morphology of *Mattimys.*

There is no indication that the zygomasseteric structure of *Mattimys* was advanced beyond the primitive protrogomorphous condition, unlike the Oligocene eutypomyids, which are sciuromorphous. The strong dental similarity of *Mattimys,* the late Eocene *Janimus,* and Oligocene *Eutypomys* makes the exclusion of the Eocene genera from the Eutypomyidae unlikely. If the zygomasseteric structure of the Eocene genera were viewed as having supergeneric significance, *Mattimys* and *Janimus* could well represent a primitive subfamily of the Eutypomyidae.

Cylindrodontidae

Wilson (1949) viewed the earliest cylindrodont, *Mysops,* from the middle Eocene, as originating from a primitive paramyine stock (=Paramyidae, *sensu* Wood, 1962). *Dawsonomys,* from the early Eocene, shares many cylindrodont characters and may represent the earliest known taxon of the family (see above discussion of *Dawsonomys*).

The cheek tooth pattern of *Dawsonomys* is not readily derivable from that of any early ischyromyid or sciuravid. It has some similarities with early Asian ctenodactyloids, such as the morphology of the trigonids of P_4 and M_1. *Dawsonomys* may have some relationship with the early Asian ctenodactyloids, but is too poorly known to suggest more than a possible relationship.

Occurrence and Radiation of Rodents in the Paleocene and Early Eocene of North America

The earliest occurrence of rodents in the world is still that of *Acritoparamys atavus* from the unique Tiffanian Bear Creek fauna of Montana. One of the unique features of this fauna is the lack of miltituberculates (see Krause, 1980). Van Valen and Sloan (1966) suggested that the early radiation of rodents in the Eocene was a major factor in the extinction of the multituberculates due to competition between these groups of animals. It is difficult to believe that the presence of a single species of rodent could have out-competed all of the multituberculates at this locality when multituberculates were still surviving elsewhere. Competition from rodents may have aided in the extinction of multituberculates, but multituberculates were already declining by the time of the first appearance of rodents.

By the earliest Eocene, ischyromyids were well diversified in both North America and Europe. Four genera, representing three different subfamilies, are present in the Clarkforkian level in the Bighorn Basin: *Paramys* (Paramyinae), *Acritoparamys* and *Apatosciuravus* (Reithroparamyinae), and *Franimys* (Pseudoparamyinae). Godinot (1981) reported three genera of three different subfamilies of ischyromyids from what he believed was equivalent in age to the Clarkforkian of France—*Paramys* (Paramyinae), *Microparamys* (Reithroparamyinae), and an indeterminate ailuravine. This clearly demonstrates the very rapid radiation of rodents at this time. There is very little difference between the Graybullian rodents and those from what has been called the Clarkforkian of the Bighorn Basin. All of the commonly occurring species of the Graybullian, *Paramys taurus, Apatosciuravus bifax,* and *Acritoparamys atwateri,* are also present in the Clarkforkian. *Paramys copei* is also present at both levels but rare. The only species that are exclusive to either level are all known by single specimens. From the Clarkforkian, *Fran-*

imys amherstensis is only known from the holotype and is not present in any Graybullian faunas. *Lophiparamys murinus, Microparamys scopaiodon* and an indeterminate reithroparamyine are represented in the Graybullian, also by single specimens. The lack of these Graybullian species in the Clarkforkian beds may be due to collecting error because all of these species are very small and may have been overlooked. The differences in the rodent faunas from the Graybullian and Clarkforkian are less than those between any of the subsequent subdivisions of the Wasatchian, suggesting that the Clarkforkian (according to the rodents) may represent the lower Graybullian of Van Houten (1945).

By Lysitean times, sciuravids become a significant part of the rodent fauna, represented by two species, *Knightomys minor* and *K. depressus.* During this time, and through the Gardnerbuttean, small reithroparamyines that were common in the Graybullian, such as *Apatosciuravus* and *Microparamys,* are rare. This lack of small ischyromyids may be due to competition from the abundant small sciuravids.

Ischyromyids begin to diversify in the Lysitean and the common species in the Graybullian, *Paramys taurus* and *Acritoparamys atwateri* disappear and *P. copei* and *P. excavatus* replace them as the dominant species. The Lysitean rodent fauna is relatively uniform throughout North America. Only a few rare species, such as *Notoparamys arctios, Franimys ambos,* and *Thisbemys* sp., are not present in all Lysitean faunas.

In the late Wasatchian, the sciuravids become quite diverse. The first appearance of *Pauromys, Sciuravus,* and two more species of *Knightomys* occurs in the Lostcabinian along with the continuation of *K. depressus* from the Lysitean. Along with the sciuravids, it is also the first appearance of the ?eutypomyid *Mattimys* and ?cylindrodontid *Dawsonomys.* Ischyromyids, however, do not undergo as rapid a radiation as the sciuravids, but show some regional variation. *Notoparamys costilloi, Thisbemys perditus, Acritoparamys pattersoni,* and *Paramys nini* are known from faunas in Colorado and New Mexico but not Wyoming. *Acritoparamys francesi* is common in the Wyoming faunas and unknown from the more southern areas. This regional differentiation might indicate a shift from a more uniform environment throughout western North America during the middle Wasatchian to more regionally restricted environments in the late Wasatchian.

The Gardnerbuttean is marked by a continuation of most Lostcabinian species, introduction of a few genera and species that continue into the Bridgerian, such as *Quadratomus, Leptotomus,* and *Reithroparamys huerfanensis,* and disappearance of some earlier forms, such as *Notoparamys* and *Paramys excavatus.* In the Bridgerian, there is an almost complete replacement of all Wasatchian species. Large manitshines and paramyines are common and sciuravids become even more diverse.

Only one species of rodent is common throughout the early Eocene, *Paramys copei. Paramys copei* is represented in all faunas from the Clarkforkian through the Gardnerbuttean, and would best serve as an index fossil for the Wasatchian (?and Clarkforkian) of North America.

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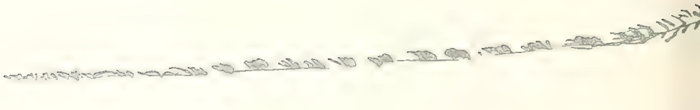

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COELACANTHS FROM THE BEAR GULCH LIMESTONE (NAMURIAN) OF MONTANA AND THE EVOLUTION OF THE COELACANTHIFORMES

RICHARD LUND AND WENDY LAURIE LUND

NUMBER 25 PITTSBURGH 1985

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ABSTRACT

The coelacanth *Rhabdoderma elegans,* type species of the family Rhabdodermatidae, is redescribed on the basis of material from the type locality at Linton, Ohio (Westphalian), other species assigned to the genus are discussed, and the rediagnosed family is assigned to the suborder Coelacanthoidei. The new genus *Dumfregia* is created for *Coelacanthus* (=*Rhabdoderma*) *huxleyi* Traquair from Glencartholm, Scotland (Visean). The osteology and ontogeny of *Caridosuctor populosum* (Rhabdodermatidae), *Hadronector donbairdi, Allenypterus montanus, Polyosteorhynchus simplex* (family Hadronectoridae, suborder Hadronectoroidei), and *Lochmocercus aciculodontus* (suborder incertae sedis), from the Bear Gulch Limestones of Fergus County, Montana (Chesterian), are described. The Devonian genus *Diplocercides* (=*Nesides*?) is assigned to the Coelacanthoidei.

Character states among the Osteichthyes are evaluated, and the possible interrelationships of the Coelacanthoidei, Sarcopterygii, and Crossopterygii are discussed.

INTRODUCTION

The osteichthyan order Coelacanthiformes includes fish ranging in age from late Devonian to recent, which differ from each other only in proportions or relatively small details of osteology. Essentially unchanged and essentially similar in all aspects are the basic body shape and fin disposition, or locomotor system, and the basic head and mouth shape, or feeding system, of all but one species, *Allenypterus montanus* (Melton, 1969). The coelacanths, therefore, are the longest surviving group of virtually unchanged vertebrates known.

The fossil record of coelacanths includes both fresh and salt water forms through the Triassic, including deposits primarily of small individuals in the Visean of Glencartholm, the Westphalian of Braidwood, Illinois (Schultze, 1972), Cannelton, Pennsylvania, and Linton, Ohio, and upper Triassic Newark supergroup of the eastern United States (Olsen and Galton, 1977). While there is some question about the salinity of the Glencartholm coelacanth beds the remainder are fresh water (Richardson and Johnson, 1971; Schram, 1976; Olsen and Galton, 1977). The Braidwood coelacanths include a number of individuals with yolk-sacs (Schultze, 1972) indicating not only that ovoviviparity was established in this group by the Pennsylvanian (Smith et al., 1975), but strengthening the suggestion that these deposits may have been spawning grounds (Thomson, 1969). Many other coelacanth-bearing deposits contain few, large specimens which have given an inadequate picture of the habitat and morphology of this group. The morphology and relationships of the Paleozoic Coelacanthiformes are particularly poorly known.

Coelacanths of five species represent approximately 15% of the fish specimens collected from the lower Carboniferous marine Bear Gulch Limestone of Montana (Lund, 1977). The fish fauna currently totals about 2,100 specimens and 76 species in four classes of which 41 species are chondrichthyan and 33 osteichthyan. One of the coelacanth species *Caridosuctor populosum,* is by far the most abundant fish in the fauna. A size and growth range can be demonstrated for three of the five species which indicates growth from birth to maturity occurred within the confines of the basin.

The ecomorphology of the Bear Gulch coelacanths has been discussed elsewhere (Lund et al., in press). This paper is limited to a consideration of their morphology and relationships and other Paleozoic coelacanths are considered in detail where this is needed to clarify these questions.

MATERIALS AND METHODS

Specimens occur in a variety of lithologies which are sequentially repeated at about 3 ft intervals throughout the 35 ft of productive limy silts quarried in the Bear Gulch member (Horner and Lund, in press). There are no detectable faunal differences in this stratigraphic interval (Scott, 1973).

The repetitive units range from a massive, extremely well indurated fine grained grey silty limestone which may laterally grade locally into beds of good fissility, downward through slightly coarser, less limy yellowish stone into a poorly indurated zone of soft, fine, pink to brown, thin bedded, irregularly fissile material best described as siltstone. One or more thin pure white caminace of non-indurated material frequently can be found at or near the base of the faule material, which is succeeded below by the next massive zone. Deposition is comparable to the lithographic limestone deposits of Bavaria (Williams, 1981).

Specimens occurring in the softer lithologies may readily be prepared by the use of needles and photographed with standard techniques. Specimens from the dense grey layers lend themselves to the removal of all bone from the head with needles and the preparation of impressions with latex (Baird, 1955). Contrast enhancement photography, using Kodak high contrast copy film at an ASA rating of 32 and three successively slower exposure times, combined with Ethol T.E.C. developer diluted 1:15 at the film's recommended developing times produced outstanding results. A blue (Wrattan 82A or equivalent) filter was also found helpful in contrast enhancement. All line drawings were prepared from a photographic base. The terminology of the skull bones follows Andrews' (1973) rhipidistian terminology wherever possible.

Specimens are deposited in the University of Montana fossil verebrate collections (MV) or the Section of Vertebrate Fossils, Carnegie Museum of Natural History (CM). Specimens have been referred to from the Royal Scottish Museum (RSM), Edinburgh, Scotland, and the Hancock Museum (HM), Newcastle, England.

SYSTEMATICS

Introduction

The Coelacanthiformes are included within the Crossopterygii on the basis of the common possession of two dorsal fins, lobed paired fins, and an intracranial joint dividing the braincase into anterior and posterior (ethmosphenoid and oticooccipital) parts. Coelacanths also share with many crossopterygians the possession of cycloid scales, a diphycercal tail, and a hyomandibula, which is not firmly held to the palate, but does aid in palatal suspension (Andrews, 1973; Jarvik, 1954). Coelacanths differ from other crossopterygians in lacking cosmine, lacking a maxilla, having a small dentary and large angular in the lower jaw, as well as in other details summarized in Table 8. While details of the interrelationship of the Coelacanthiformes with other crossopterygians are vague, only Miles (1977) in recent years has questioned the basic interrelationships. Evidence bearing on this question will be discussed further in this paper in light of the coelacanths described below, but there is no convincing evidence on which to base removal of the Coelacanthiformes from the Crossopterygii.

The Subordinal Question

The order Coelacanthiformes derives its name from the first described species, *Coelacanthus granulatus* Agassiz, from the Permian Marl Slate of Durham and Northumberland, England (Agassiz, 1837; Moy-Thomas and Westoll, 1935). Three suborders have been named, the Diplocercidoidei, Coelacanthoidei, and the Laugioidei (Obruchev, 1967). The suborders are based principally on chronology, with all Devonian and Carboniferous coelacanths except the Carboniferous *Coelacanthus* species being included in the diplocercidoids. All post-Carboniferous coelacanths except *Laugia* (Stensiö, 1921) are considered coelacanthidoids (Obruchev, 1967). *Laugia* has been placed in its own suborder solely on the basis of a pelvic girdle modified for attachment to the pectoral girdles. This character complex alone hardly has the morphologic, functional, or phylogenetic level of significance which normally would accompany subordinal separation (Greenwood et al., 1966).

Two families have been included in the Diplocercidoidei, the Devonian Diplocercidae (Stensiö, 1937) and the Carboniferous Rhabdodermatidae (Berg, 1958). The major subordinal criteria have been: a solidly ossified braincase versus reduced braincase ossifications; presence or absence of a suboperculum; presence of a basipterygoid process; size of the ectopterygoid and the size of the vomers. Only *Diplocercides* of the Diplocercidae possesses a solid braincase and a basipterygoid process (Stensiö, 1937; Bjerring, 1973), rendering these characters useful at the generic level if at all. As discussed below, the elements which have been called the suboperculum and preoperculum in coelacanth literature (Schaeffer, 1952) are actually homologous to the preoperculum and quadratojugal, respectively, of crossopterygians (Andrews, 1973). No coelacanths described prior to the Bear Gulch forms have a suboperculum and the character as previously used is incorrect. The size, or even the presence, of the ectopterygoids and vomers cannot be satisfactorily demonstrated in many coelacanths, and the contention that large vomers are primitive (Obruchev, 1967) is contradicted by Andrews (1973). Neither character seems to be consistent or useful at any taxonomic level higher than genus. To summarize, prior to the introduction of the new evidence in this paper, the criteria for coelacanth suborders are either significant at the generic level only, trivial, or incorrect. The suborders previously proposed have no taxonomic applicability.

Paleozoic Taxa of Family Rank

The Diplocercidae, Rhabdodermatidae and Coelacanthidae have been named in reference to *Diplocercides kayseri* from the Devonian (Stensiö, 1922), *Rhabdoderma elegans* from the Pennsylvanian (Berg, 1958), and *Coelacanthus granulatus* from the Permian (Agassiz, 1839), respectively. *Coelacanthus granulatus* typifies the problems which have existed among coelacanths. Morphological information on the type species of the type genus, and therefore the lynchpin of coelacanth studies, was limited to the posterior dermal cranium and postcranial skeleton (Moy-Thomas and Westoll, 1935) until Schaumberg's revision in 1978. The cranial information, which follows, is taken from Schaumberg (1978), the postcranial from Moy-Thomas and Westoll (1935).

The premaxillae consist of several splint-like tooth plates, and bones of the rostral area are small, numerous and loosely associated, hence poorly known. The skull roof of the ethmosphenoid region has a large postrostral flanked by three or four paired frontonasals, followed by a pair of parietals; the skull roof itself is flanked by a single series of supraorbital canal bones. The infraorbital canal bones consist of a large lateral rostral, a lacrimojugal and a postorbital, but an antorbital is lacking. There are three bones in the cheek, an isolated quadratojugal, and a squamosal and preoperculum reduced to lateral line canal tubes. A suboperculum is lacking.

The skull roof of the otico-occipital consists of long postparietals and posterolateral tabulars, followed by a small posttemporal and seven extrascapulars along the posterior edge. The supraorbital lateral line is restored as joining the infraorbital canal at the lateral rostral anteriorly and the otic canal in the postparietal posteriorly.

The shoulder girdle contains an anteriorly directed, triangular supracleithrum, large cleithrum, laterally overlapping extracleithrum, and clavicle. The pelvic plate sutures to the contralateral element via a posterior, mesially directed process, articulates with the fin axis via a posterolateral expansion and bears a thin anteromesial lamina strengthened by two ridges. The anal plate is simple, and lies parallel to the body wall midway between pelvic and anal fins. The first dorsal fin plate is rounded above, with a straight lower edge, while the second dorsal plate resembles a posteriorly reclining T, the lower limb of which rests in a notch formed by several shortened neural spines. There is a one-to-one relationship between the caudal fin rays and their endoskeletal supports. There are bony ribs.

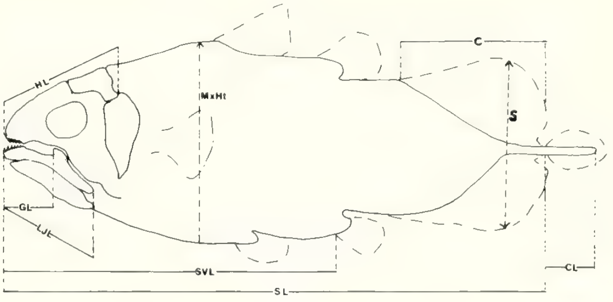


Fig. 1.—Measurements. Abbreviations: C, chord; CL, length of caudal lobe; GL, gape length; HL, head length; LJL, lower jaw length; MxHt, maximum height; S, span (aspect ratio of tail = span/chord); SL, standard length; SVL, snout–vent length.

Schaumberg concludes (1978) that *Latimeria* is sufficiently close to *C. granulatus* that they both belong in the family Coelacanthidae. While there are difficulties in accepting Schaumberg's restoration of the ends of the supraorbital canal, for reasons elaborated on in the subsequent discussion, our analysis completely agrees with his conclusions.

All Permian and Mesozoic coelacanths have previously been included in the family Coelacanthidae except *Laugia* (Berg, 1958; Obruchev, 1967; Romer, 1966), the Laugiidae being distinguished on the basis of its unique pelvic girdle. As considerable cranial information exists on Mesozoic coelacanths (Schaeffer, 1952, 1967), the new diagnosis of *C. granulatus* now permits a revision of the Mesozoic coelacanths as well as an attempt to analyze and compare the other nominal coelacanth families.

The family Rhabdodermatidae has had a checkered history. J. S. Newberry (1856, 1873) described three species of coelacanths, *Coelacanthus elegans, C. ornatus* and *C. robustus,* from the cannel shale below the Upper Freeport Coal, late Westphalian D, of the Linton mine, Jefferson County, Ohio. *C. elegans* was distinguished from *C. ornatus* by finer vermiform scale ornamentation. *C. robustus,* known only from fragmentary large specimens, was suggested to be the adult of *C. elegans* by Newberry (1873).

The genus *Rhabdoderma* was erected by Reis (1888), *C. elegans* being designated the type species. Moy-Thomas (1937) placed *R. ornatus* and *R. robustus,* as well as several other coelacanths from the American and European late Carboniferous into synonymy with *R. elegans* on the basis of scale ornamentation and fin plates. Moy-Thomas presented a revised description of the species, with a restoration (Moy-Thomas, 1937, fig. 1) which is devoid of reference to the horizons, localities, or specimen numbers used in its construction. This is the only nearly complete restoration of a Carboniferous coelacanth in print and has served as the basis for the family Rhabdodermatidae of Berg (1958) as well as all subsequent attempts to analyze the evolution of the Coelacanthiformes (Schaeffer, 1952; Echols, 1963; Obruchev, 1967; Andrews, 1973).

Over 135 acid cleaned and latex peeled *Rhabdoderma* have been prepared from specimens collected by my field parties at Linton, Ohio. These specimens, now in the collection of Carnegie Museum of Natural History, Pittsburgh, range in size from a complete individual of 49 mm total length to a poor skull of a fish of estimated 321.6 mm total length. It is clear from analysis of the specimens that there is only one species, *R. elegans,* in the Linton deposits. It is also clear that *R. elegans* is not the species described and illustrated by Moy-Thomas (1937).

Having synonymized a number of nominal species with *R. elegans* principally on the basis of ornamentation, Moy-Thomas (1937) incorporated the remainder of the British Carboniferous species into the genus and named four new species on the same basis, from few isolated bones. One species, *Coelacanthopsis curta* Traquair (1905), however, was considered "indeterminable" by Moy-Thomas. Reexamination of the type and only known specimen of *Coelacanthopsis curta* by the authors does not clarify the osteology of the head. It is clear, however, that the midsection of the body is faulted away, and that the tail clearly shows a greater number of fin rays than endoskeletal supports.

Diplocercides kayseri Stensiö (1922), the only species of the genus, typifies the family Diplocercidae. The postrostral skull roof, cheek, braincase, shoulder girdle, body and fin outlines are known and well studied, whereas pelvic and median fin plates are unknown. Small paired frontonasals, with irregular median postrostrals, lie over the ethmoid region and long parietals over the orbits. The skull roof posterior to the intracranial joint is essentially as in *Coelacanthus granulatus* except that the operculum does not articulate directly with the tabular. The cheek consists of four bones, which lack tight joints, and the operculum is the sole bone of the opercular flap. The shoulder girdle, as preserved, consists of cleithrum and clavicle without an extracleithrum. There are more caudal fin rays than endoskeletal supports. A basipterygoid process and a posteriorly projecting antotic process link the palate to the ethmosphenoid portion of the neurocranium (Bjerring, 1973), and the two portions of the neurocranium are solidly ossified.

A degree of confusion exists about the systematics and morphology of *Diplocercides* and *Nesides schmidti* (Stensiö, 1937). Stensiö states that he selected a specimen from among several *D. kayseri,* sectioned it, and subsequently decided that it was sufficiently different from unsectioned and less complete *D. kayseri* to warrant the erection of a new genus and species. There are certainly differences; some, like degree of endocranial ossification, can be accounted for by differences in growth stages, and some, like dentition, could be either preservational or of taxonomic significance. The relationship between the two genera, however, remains to be adequately explored and the significance of the degree of endocranial ossification becomes dubious.

To summarize family-level taxonomy and systematics of the coelacanths is relatively easy. There is no way to distinguish the Rhabdodermatidae from the Coelacanthidae on the basis of currently published information. Diplocercidae differ from Coelacanthidae in having: a greater than one to one ratio of fin rays to endoskeletal supports; several median elements in the postrostral region; four, somewhat larger, but loose cheek plates; a small basipterygoid process; and possibly in having a greater degree of endocranial ossification in the adult stage.

One of the five Bear Gulch Limestone coelacanths, *Caridosuctor populosum,* has a suite of characters enabling its assignment to a recognized family, the Rhabdodermatidae. The remaining three well-preserved species agree in the common possession of a character suite uniquely primitive among described coelacanths and as such, represent a discrete taxonomic unit. This taxonomic unit will be considered as a single family and suborder, in contrast with the coordinate unit containing either more derived but presumed extinct Diplocercidae, the contemporaneous Rhabdodermatidae, or the problematical species "*Coelacanthus*" *huxleyi.* The members of this new suborder share no obvious advanced characters, do not fall into any morphological arrangement suggestive of subordinate taxonomic groupings, and are not comparable to any fish outside the Bear Gulch fauna. They do, however, occupy a unique morpholgical and evolutionary position among the Coelacanthiformes.

The following suite of characters is used as guidelines for familial diagnoses: condition of the premaxilla and the rostral bones; presence or absence of the antorbital; number of series of bones of the supraorbital canal; presence and condition of supratemporal; number of bones and association in the cheek; presence or absence of a basipterygoid process; presence or absence of a suboperculum; condition and position of the pelvic, anal, and second dorsal fin plates; and the ratio of caudal fin rays to endoskeletal supports.

SYSTEMATIC PALEONTOLOGY

Order Coelacanthiformes
Suborder Coelacanthoidei

Type family.—Coelacanthidae Agassiz, 1839.

Diagnosis.—Nasal-frontal-parietal series of bones flanked laterally by a single supraorbital canal series of bones, the supraorbital canal lies lateral to the margins of the nasoparietals. A supratemporal bone either greatly reduced or absent. May be five or fewer, loosely associated bones in cheek. Opercular flap supported only by an opercular bone. Second dorsal fin articulates with posterodorsal margin of its basal plate. Anal fin plate located in ventral body wall anterior to firs haemal spines, and posterior to anus.

Included families.—Coelacanthidae (type), Rhabdodermatidae, Laugiidae, Diplocercidae.

Family Rhabdodermatidae Berg, 1958

Type genus.—*Rhabdoderma* Reis, 1888.

Diagnosis.—Paired premaxillae unornamented, ascending lamina of each perforated by a large pore for rostral organ. Bones of ethmoid commissure and rostral area small, unornamented, loosely in contact with each other and border large lateral line canal pores. Frontonasals paired, ornamented, and meeting in dorsal midline. Single series supraorbital canal bones lies lateral to frontonasals and parietals. Antorbital present, perforated by two rostral organ pores, and bordering posterior narial opening posterodorsally. Infraorbital canal bones as in Coelacanthidae, the postorbital set posterior to intracranial joint. Cheek bones five in number, thin, completely covering the cheek, with tight or overlapping sutures. Operculum the sole bone in opercular flap. Skull roof of the oticooccipital portion consists of a pair of long postparietals, flanked by reduced supratemporals anterior to posterolateral tabulars. Postparietals contain a lateral and a posterior pit line. Supratemporal contains anterior half of otic canal, which joins infraorbital canal from postorbital and passes into tabular posteriorly. Five extrascapulars present. Anocleithrum apparently not in contact with the braincase. Median and paired fin supports essentially as in Coelacanthidae except that pelvic plates are extended anterolaterally and anal fin support may not ossify. Caudal fin rays each have one endoskeletal support.

Genus ***Rhabdoderma*** Reis, 1888

Type species.—*Coelacanthus elegans* Newberry, 1856.

Diagnosis.—Premaxilla with few, large teeth, other tooth bearing bones of palate and lower jaw with fine granular teeth. Lateral borders of frontonasals and parietals indented to receive supraorbital canal bones, and each supraorbital pore bordered by parts of three bones. Tabular projects posteriorly beyond rear margin of postparietal. Preopercular canal in squamosal bears prominent pores dorsal to intersection of ascending and anterior canal branches. Shoulder girdle unornamented in smaller individuals. Anal fin support unossified. Ornamentation on skull roof (except tabular) antorbital and postrostral of fine tubercles, preoperculum of coarse tubercles, and remaining head bones of fine linear ridges.

Included species.—*R. elegans* Newberry, 1856; *R. lepturus* Huxley, 1866.

Remarks.—A morass of names have been proposed in the past, on the basis of isolated bones from the British Coal Measures (Moy-Thomas, 1935, 1937). There seems to be no way to define any of them with material presently available. *R. exiguum* (1908), while represented by several whole specimens (Schultze, 1972) has never been adequately described and is best omitted from any definite assignment at present.

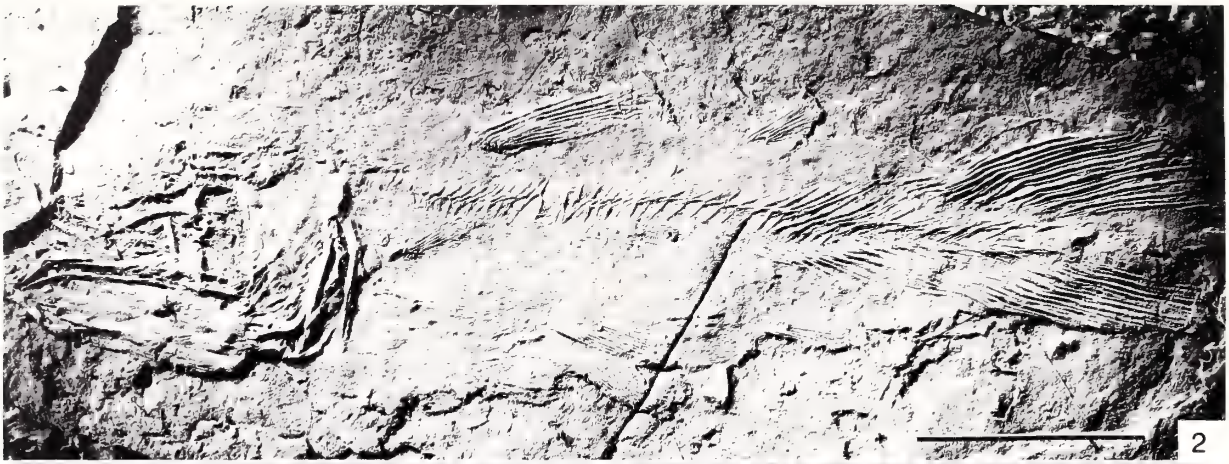
Rhabdoderma elegans Newberry
(Figs. 2–12)

Synonymy.—*R. ornatus* Newberry, 1856. (*R. robustus* Newberry, 1856.)

Cotypes.—AMNH 503, 656.

Horizon and locality.—The cannel shale below the Upper Freeport coal, Allegheny Group, Late Westphalian D, from the Linton mine, Saline Township, Jefferson County, Ohio.

Diagnosis.—Moderate sized *Rhabdoderma,* up to 32 cm in length, with three paired frontonasals, two



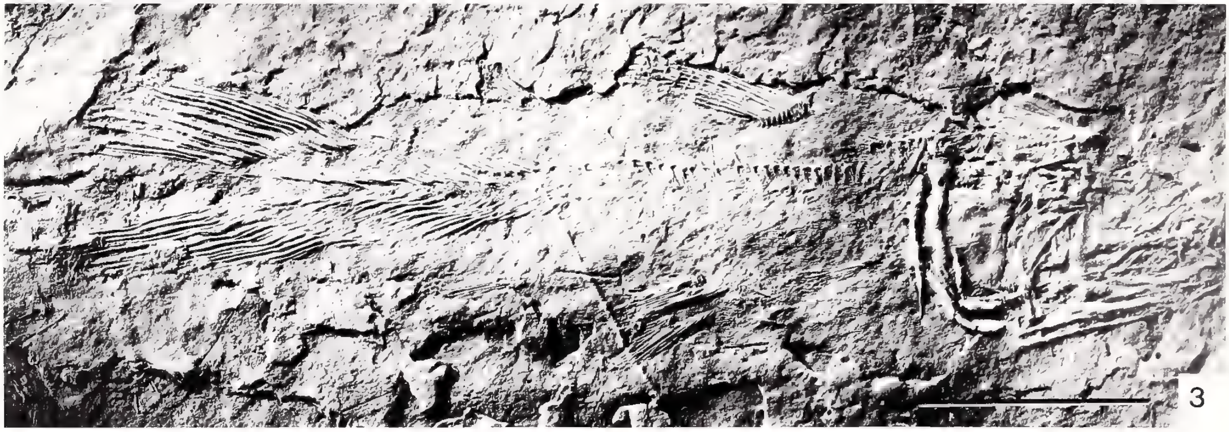
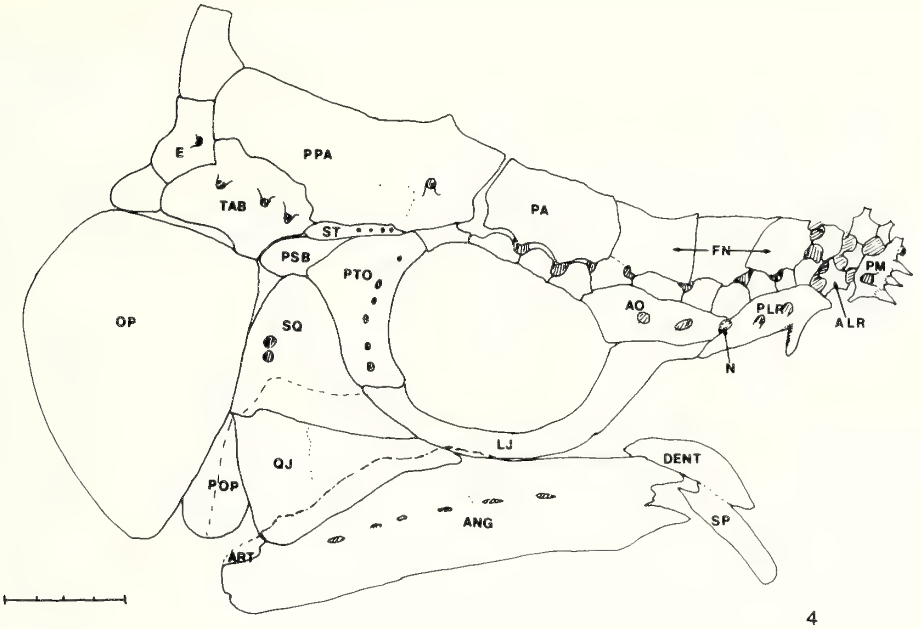


Fig. 2.—*Rhabdoderma elegans,* CM 23025a. Scale = 1 cm.
Fig. 3.—*Rhabdoderma elegans,* CM 23025b. Scale = 1 cm.

anterolateral rostrals, four supraorbitals between postorbital and antorbital, and eight anterior supraorbitals. Terminal pore of supraorbital canal and transverse and posterior pit lines are prominent. Supratemporal narrow and bears several otic canal pores, tabular bears two to three large dorsomesially directed pores. Ethmoid region broad and shallow, postorbital, squamosal and quadratojugal are tall. Squamosal bears two large pores dorsal to anterior limb of the preopercular canal. Quadratojugal, angular and gular bear transverse pit lines. Operculum taller than wide. Skull ornamentation of tightly packed tubercles and ridges from the onset of ornamentation through adulthood. Palatal dentition of fine, slightly diverging lines of denticles, dorsally arched and fusing into thin ridges posteriorly. Body slender, pelvic plate extended anterolaterally by three processes. Anal plate unknown, and fin rays unornamented.

Description

Occurrence.—*Rhabdoderma elegans* is abundant at the Linton locality, but most specimens range in size from around 10 to 20 mm in gular length. Few are preserved with intact bodies and the small size of individual blocks of matrix results in the retrieval of very few complete fish. A complete specimen of 10.4 mm gular length (Figs. 2, 3), 49 mm in standard length, shows only the first few tuberculations developing on the postparietal and was evidently a very young individual. The largest known specimen (CM 23012) is a poorly preserved head with a gular length of 56.7 mm. Assuming linear growth relationships a standard length of 321.6 mm can be estimated for CM 23012. There are few elements of intermediate size between the two extremes. It is quite plausible that the Linton oxbow lake served as a spawning ground for *Rhabdoderma* females.



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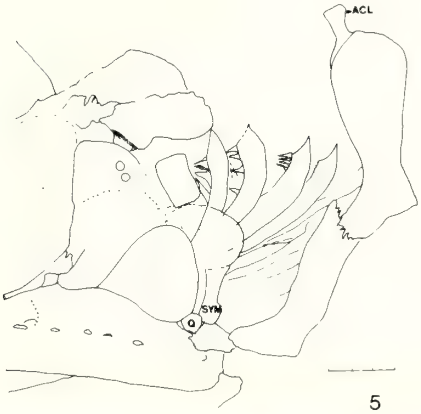

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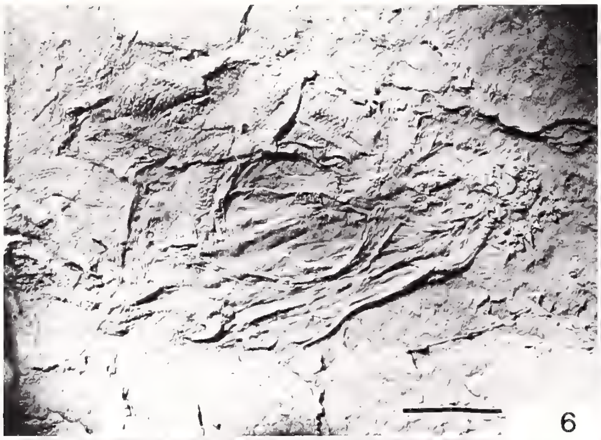
Fig. 4.—*Rhabdoderma elegans,* head restoration based on CM 23178, 23179, and 23180. Scale in mm. Abbreviations: ALR, anterolateral rostrals; ANG, angular; AO, antorbital; ART, articular; DENT, dentary; E, extrascapulars; FN, frontonasal series; LJ, lacrimojugal; N, naris; OP, operculum; PA, parietal; PLR, posterolateral rostral; PM, premaxilla; POP; preoperculum; PPA, postparietal; PSB, prespiracular; PTO, postorbital; SP, splenial; SQ, squamosal; ST, supratemporal; TAB, tabular.

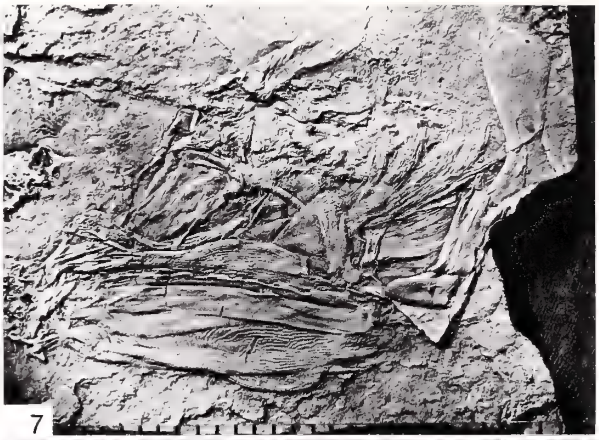
Fig. 5.—*Rhabdoderma elegans,* CM 23179b, branchial region. Scale is in mm. Abbreviations: ACL, anocleithrum; Q, quadrate; SYM, symplectic. See Fig. 7.

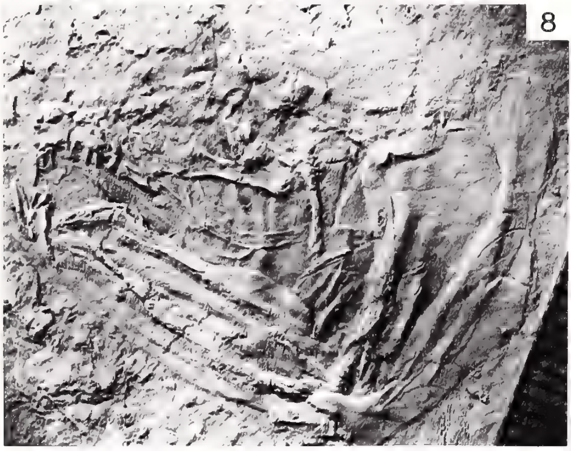
The spacing of ornamentation on the skull bones is highly variable among small individuals of the same or similar sizes (Figs. 6–11). Growth of individuals evidently resulted in the addition of more tubercules with little increase in their size, although there seems to be a fair measure of individual variation in tubercle size itself. Bones of the largest individuals are densely tuberculated.

Ethmosphenoid.—The premaxilla (Figs. 6, 8) bears three or four teeth and usually shows one additional tooth base, an indication of a possible replacement position. The premaxilla articulates by narrow facets with a small median rostral and two anterolateral rostrals. The dorsal border of the premaxilla is emarginated between the facets for large pores, and there is a deep notch between the posterior end of the premaxilla and the posterolateral rostral where the anterior narial opening of *Latimeria* is located (Millot and Anthony, 1958).

The rostral is followed in the midline by a slightly







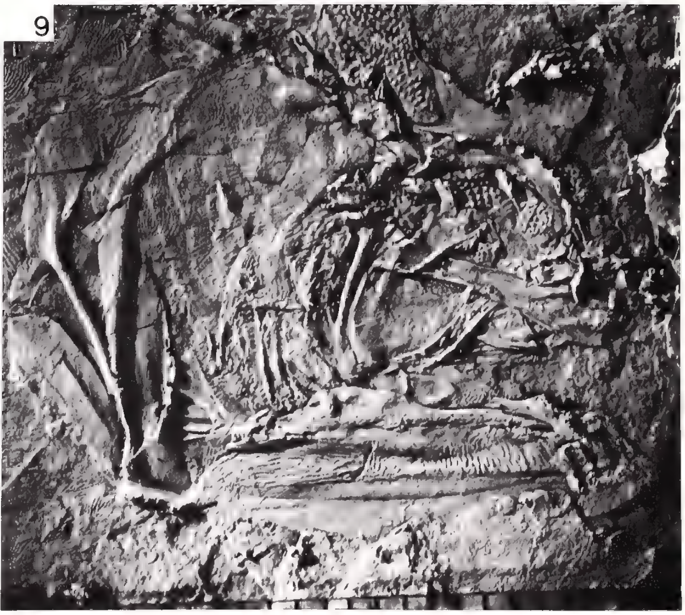
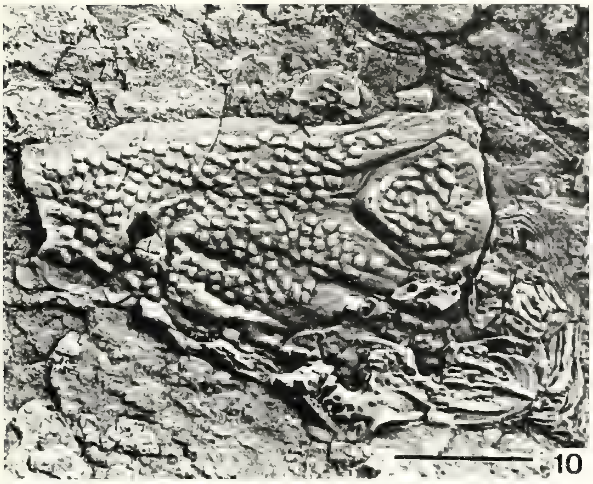


Fig. 6.—*Rhabdoderma elegans,* latex peel of head, CM 23179a. Scale is 5 mm.
Fig. 7.—*Rhabdoderma elegans,* latex peel of head, CM 23179b. Scale in mm.
Fig. 8.—*Rhabdoderma elegans,* latex peel of head, CM 26250. Scale in mm.
Fig. 9.—*Rhabdoderma elegans,* latex peel of head, MV 5564. Scale in mm.

larger, highly emarginated median postrostral. Posterior to the rostro-postrostral series are two other small, emarginate bones, the most anterior of the supraorbital canal bones. These bones are bordered posteriorly by the anterior edge of the frontonasal, and the more mesial of the two articulates by small facets to the adjoining elements. Three series of large pores, therefore, can be seen to traverse the snout between the frontonasals and the premaxillae, in addition to the premaxillary pore.

The three frontonasals are flanked laterally by eight anterior supraorbital elements (the tectals of Jarvik, 1942), and the supraorbital canal pores each occur between the edge of the frontonasal and two adjacent anterior supraorbitals. Lateral to the supraorbitals, bordering the two anterior frontonasals and posterior to the anterolateral rostrals is the large, thin posterolateral rostral. A conspicuous process projects ventrally from the anterior aspect of its ventral border (Fig. 4). This process forms the posterior border of the anterior nostril in *Latimeria* (Millot and Anthony, 1958), *Macropoma* (Watson, 1921) and can also be found in the Devonian *Onychodus* (Andrews, personal communication). Two large pores of the infraorbital lateral line canal perforate the posterolateral rostral, and its posterodorsal edge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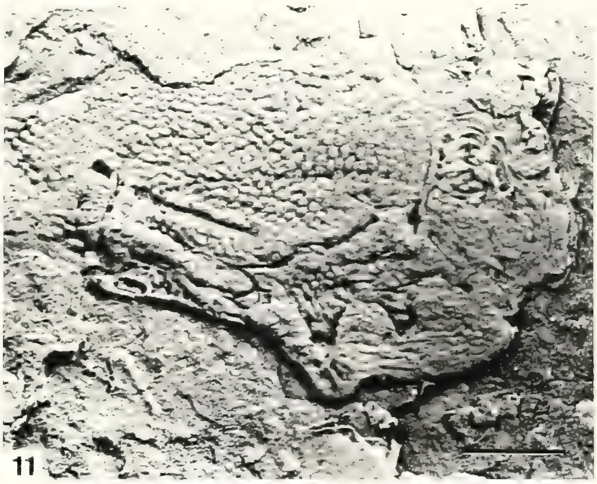
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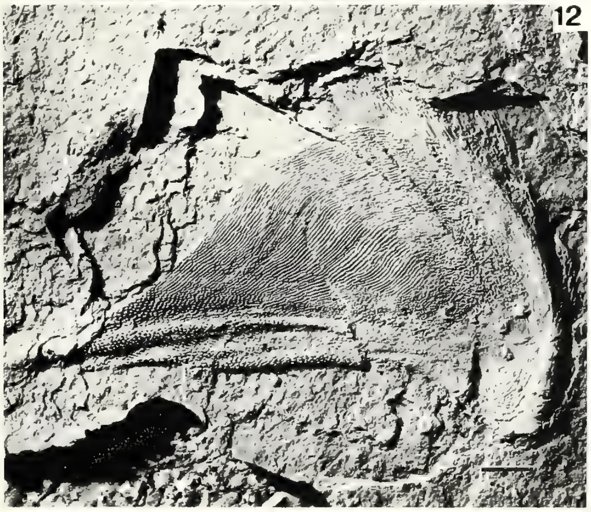
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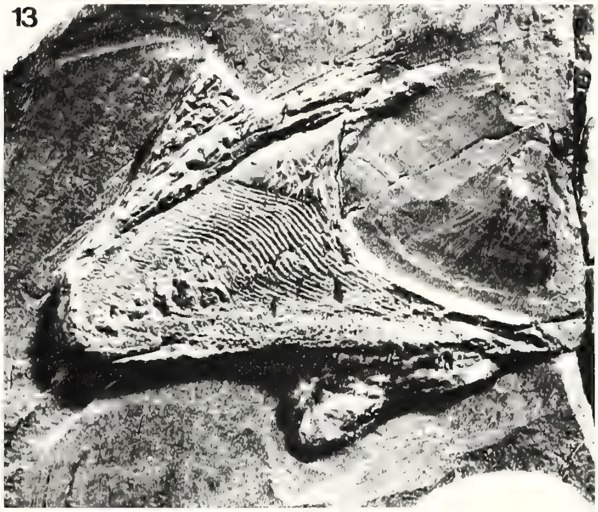
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Fig. 10.—*Rhabdoderma elegans,* latex peel of left skull table with supernumary bone, CM 35246. Scale is 2 mm.

Fig. 11.—*Rhabdoderma elegans,* latex peel of left skull table with two supernumary bones, CM 25228. Scale is 2 mm.

Fig. 12.—*Rhabdoderma elegans,* latex peel of right endopterygoid, CM 23631b. Scale is 2 mm.

Fig. 13.—*Rhabdoderma lepturus,* latex peel of left endopterygoid, Hancock Museum 960-31.

is notched, in correspondence with a notch in the antorbital, in a position corresponding with the location of the posterior nostril of *Latimeria* (Millot and Anthony, 1958). The antorbital is long and low, perforated by two large pores corresponding in position to rostral organ pores of *Latimeria.* It is bordered ventrally by the anterior end of the lacrimojugal and anteroventrally by the posterolateral rostral. The most anterior of the three true supraorbital bones fit onto the posterodorsal corner of the antorbital. The short parietal covers the interorbital area, bearing an anteroventrally projecting ethmoid lamina. The antotic process projects posterolaterally from under the posterolateral corner of the parietal. The posterior supraorbital lies lateral to the postparietal and antotic process, posterior to the intracranial joint.

The dermal bones of the ethmosphenoid region abut against each other loosely across the dorsal midline as well as elsewhere. There are no firm, tight contacts between any two bones in any individuals of any size. There is considerable variability in the relative sizes and shapes of the contralateral frontonasals as well as among individuals.

Cheek.—The postorbital, squamosal, lacrimojugal, and quadratojugal are well ossified, with overlapping or firmly butted junctions. The prespiracular is thin and fits directly against the curved anteroventrolateral lamina of the tabular in a manner which leaves no doubt that it formed a spiracular operculum (Fig. 6). The preoperculum is a thin bone with relatively few, coarse tubercles (Fig. 9). The preoperculo-mandibular lateral line canal traverses the preoperculum and part of the squamosal vertically, ending in two large pores in the squamosal (Figs. 6, 8, 9). Below these pores a horizontal limb carries the main canal forward to join the infraorbital at the postorbital-lacrimojugal junction. A vertical pit line is found in the quadratojugal.

The infraorbital canal joins the otic canal at the anterior end of the supratemporal at the level of the lateral pit line of the postparietals (Figs. 4–6, 10, 11). There is no evidence in favor of a direct junction between supraorbital and otic canals. The supratemporal is loosely sutured to the postparietal. The contralateral postparietals abut loosely in small individuals but develop an anterior peg-and-socket suture with growth. At least four of 60 postparietals examined show evidence of an additional bone along the rear margin of the skull roof (Figs. 10, 11): this element tends to be obliterated by subsequent growth of bone and ornamentation. It is possible that it is this sort of supernumary bone that was found by Wenz (1975). A single specimen (Fig. 11) shows evidence of a duplicate supratemporal mesial to the canal bearer.

The dentary is thin, bears a few fine granular teeth, and forms the anterior edge of the broad lower jaw. A short vertical pitline rises from the mandibular canal directly under the coronoid bone. The splenial and the angular bear large mandibular canal pores. The coronoid (Figs. 6–9) is quadrangular and relatively long based, with a prominent dorsally oriented saddle and a noticeable anterior inclination. The coronoid bears circumferential rows of fine teeth on its oral surface, and fits mesial to the lacrimojugal immediately anterior to the quadratojugal. The coronoid of *Latimeria* supports extensive labial folds at the corner of the mouth. There is an extensive area of overlap between angular and gular (Figs. 7–9) ventral to the canal pores. The symplectic is long and prominent, and the single articular has both dorsally and mesially facing facets for the quadrate as well as a more posterior articulation for the symplectic. The retroarticular is separately ossified (Fig. 9) in smaller individuals.

The main features of the shoulder girdle are displayed in Figs. 7–9, but it should be noted that the anocleithrum is short, stubby, and does not seem to contact any element of the cranium. Only the largest cleithra (CM 23012) show ornamentation on their posterodorsal corners. The gills are arranged as in *Latimeria* (Millot and Anthony, 1958) (Fig. 7), and bear clusters of sharp teeth.

Postcranium.—The axial skeletons of small specimens show 30 thoracic and 18 ossified caudal vertebral arches (Figs. 2, 3) although larger specimens may show up to four more posterior arches. The first nine or 10 neural arches are wide with very short neural spines and constitute a functional cervical region. The first dorsal fin plate (rarely visible and never clear) originates at the end of the cervical region, and the second dorsal support is intercalated between neural spines in the area around segments 26 and 27. The dorsal and ventral lobes of the caudal fin originate at around segment 35, with one or two free floating endoskeletal supports of the reduced leading rays. There are almost invariably one or two more rays in the dorsal (2–3+10–11) than in the ventral lobe (2–3+9–10) of the caudal fin. The rays of the fins are only distally segmented, and fin outlines are rounded.

The pelvic fins contain numerous rays. The pelvic plates were braced across the midline by a mesial process with an interdigitating suture, and anterolateral processes of the pelvic plate braced the pelvis in the body wall (Fig. 73). The anal plate is unknown. The second dorsal plate is very thin with no well developed articular area, but the axis of the fin evidently attached at the posterodorsal edge, as in modern coelacanths.

Discussion.—Forey (1981) has redescribed material from the British Carboniferous under the name of *Rhabdoderma elegans.* The principal diagnostic characters are the "kidney shaped" first dorsal fin plate, which cannot be demonstrated in the type material, and the convergent ornamentation of the scales, which is of dubious value. There are also several serious anatomical differences between *Rhabdoderma elegans* as defined on the basis of material from the type locality, and the British material that may preclude a relationship even at the generic level. The coronoid of *R. elegans* is quadrangular, although with a dorsal saddle and some forward inclination, whereas the coronoid of the British species is interpreted as triangular. The supraorbital canal connects to the otic canal in the tabular via a transverse supraorbital commissure traversing the edge of the postparietal in the British species, whereas in *R. elegans* there is no visible canal in the postparietal and there is a small free supratemporal between postorbital and tabular. The terminal pore of the supraorbital canal is prominent in *R. elegans* but not present in the British species.

Further, the transverse and posterior pit lines differ strongly between the two species. The tabular of *R. elegans* projects well beyond the rear margin of the postparietal and is perforated by few, large pores for the otic canal, features not seen in the British material. There are also differences in the squamosals, the numbers of vertebral arches and the proportions of the cleithrum, extracleithrum and clavicle. Finally, *Rhabdoderma elegans* apparently lacks an ossified anal plate. Although the snout of the British species is obviously very incompletely known, the premaxilla is very similar to that of other known Rhabdodermatidae in bearing a perforation for the rostral organ. Contrary to Forey's assertion, however, there is no evidence that the ethmoid commissure was carried by the premaxilla (see below). The British species cannot reasonably be assigned to the genus *Rhabdoderma,* and certainly cannot be considered conspecific with *R. elegans.*

Comments on Rhabdoderma lepturus

A few specimens of whole and partial heads of *R. lepturus* (Huxley, 1866) from Newsham Colliery, Northumberland, were available for study. The quality of preservation of these specimens did not permit detailed comparison with *R. elegans*, and the specimens were preponderantly from moderate and large-sized individuals. *R. lepturus* differs from *R. elegans* in a number of small details, such as: having a tabular which projects less prominently both laterally and posteriorly; a posterior pit line continuous nearly to the posterior margin of the skull; and in having increasingly sparse ornamentation on the parietals, postparietals and gulars with increasing size. The gulars also lack a prominently tuberculated mesial zone and have a greater area ornamented by transverse ridges. The palates differ in proportions (Figs. 12, 13). The pelvic girdle of *R. lepturus* differs in having a long, angular articular process and the second dorsal fin plate resembles the coelacanthid condition. There are no obvious differences in premaxillae, lower jaws or shoulder girdles. It would be difficult at present to distinguish small individuals of the two species without better specimens.

Comments on Coelacanthus huxleyi

Traquair (1881) described a new species of coelacanth from the Visean of the Esk Valley of Dumfriesshire, Scotland, on the basis of a number of small individuals. The largest individual is only 76 mm in standard length and preservation of the skulls is poor. Sufficient cranial and postcranial information is available however (even in Moy-Thomas, 1937) to recognize that the unique morphology of "*C.*" *huxleyi* necessitates its assignment to a new genus outside the scope of coelacanth families as presently understood.

Incertae Familiae

Genus ***Dumfregia,*** new genus

Type species.—Coelacanthus huxleyi Traquair, 1881.

Diagnosis.—Small coelacanths with skull roof firmly sutured across the midline and longitudinally furrowed. Antorbital present, suboperculum lacking, and palate suspended directly below intracranial joint, indicating a very short antotic process. Dermal ornamentation appears confined to few coarse longitudinal lines on the gular; operculum and skull roofing bones smoothly finished. Six cervical, 19 trunk and up to 22 caudal neural arches. Ossified ribs present in trunk. First dorsal fin originates over eighth neural arch and stem of second dorsal fin intercalated above 23rd neural arch. Basal plate of second dorsal fin is rounded and fin axis originates directly above basal plate. Pelvic plate long and composed of a trough-like element appearing to be lamellar bone anterior to a short, cancellous looking region with short narrow processes facing posteriorly and laterally; the two plates broadly joined in the midline. Anal plate with ventral lamina and a posterodorsal process braced against first complete haemal spine. There are 3–4+11–13 dorsal caudal rays, +12–14 ventral caudal rays, and an equal number of endoskeletal supports.

Etymology.—Dumfregia, latinization of Dumfries, the shire in which the specimens were found.

Dumfregia huxleyi (Traquair)
Figs. 14, 15

Synonymy.—
Coelacanthus huxleyi Traquair, 1881.
Rhabdoderma huxleyi Reis, 1888.
Coelacanthus huxleyi Woodward, 1891.
Coelacanthus huxleyi Aldinger, 1931.
Rhabdoderma huxleyi Moy-Thomas, 1937.
Rhabdoderma huxleyi Forey, 1981.

Type specimen.—IGS-GSE 4693.

Referred specimens.—IGS-GSE M2149, 2297c, 5644, 5645. RSM 1885-54-6, 1885-54-7, 1885-54-9, 1891-53-4, 1978-43-1.

Horizon and locality.—Visean C_2S_1 Lower Carboniferous Glencartholm volcanic beds, Upper Border Group in the river Esk, Dumfriesshire, Scotland.

Diagnosis.—As for genus, the only known species.

Discussion.—Unlike the Rhabdodermatidae, the

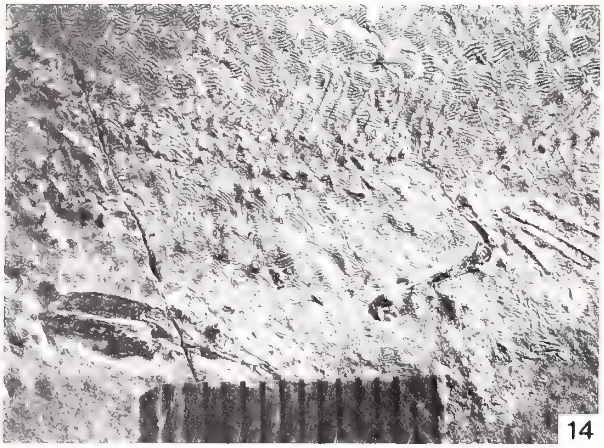
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Fig. 14.—*Dumfregia huxleyi,* midbody, RSM 1885-54-9. Scale in mm.

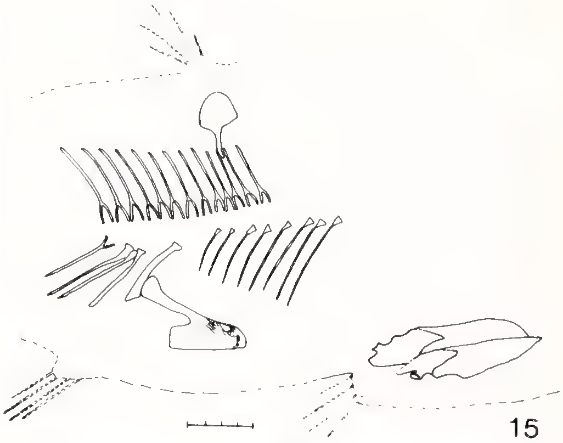
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Fig. 15.—*Dumfregia huxleyi,* midbody, RSM 1885-54-9. Scale in mm.

head of *D. huxleyi* shows no evidence of ornamentation and is not roofed with loosely abutted, flat bones. It is, instead, constructed of two highly sutured units longitudinally grooved to maximize resistance to bending deformation. The architecture of the head, as known, resembles that of coelacanthids although an antorbital seems to be present. It is interesting, if of unknown significance, that prominent otoliths are preserved in virtually every skull. An ossified swim bladder is occasionally in evidence.

The second dorsal fin plate (Figs. 14, 15) is a rounded, thin plate upon a thin intercalary stem, and unlike either rhabdodermatid or coelacanthid conditions the fin axis does not arise from the posterodorsal limb of a T-shaped plate, but directly above the rounded plate. The primitiveness of this character will be discussed later in this paper.

The pelvic plates are evidently compound structures in origin with an anterior troughlike lamellar-bone plate and a posterior unit. They are far simpler in morphology than rhabdodermatid plates in lacking any anterolateral or medial processes. While coelacanthid pelvic plates also bear a medial process (Fig. 73), they, like *Rhabdoderma,* show a cancellous zone only at the articulation of the axis of the fin. Only *Undina minuta,* as illustrated by Schaeffer (1941), has a similar pelvic plate, although Stensiö (1921) indicates that the pelvic plates of *Laugia* might be compound as well as complex.

All previously described coelacanth anal plates have been unsupported in the ventral body wall anterior to the first haemal spines. The bracing of the anal plate against the haemal front is an approach to the primitive condition of endoskeletal support as seen in several Bear Gulch coelacanths, in Rhipidistia (Andrews, 1973), and in Actinopterygii (Lowney, 1980). There is a unique mixture of advanced and relatively primitive characters in *Dumfregia* that makes it difficult to place in the context of coelacanth systematics at present.

The Glencartholm volcanic beds are generally considered to be marine on the basis of their invertebrate fauna (Lumsden et al., 1967). It must be noted that collection was accomplished with the aid of blasting powder which tended to obscure precise stratigraphic relationships. The presence of apparently fresh water ostracods among the coelacanths reinforces the observation that the marine invertebrates and many of the fish do not occur in the same layers (R. B. Wilson, personal communication). It is plausible to postulate an estuarine or other mixed environment for *Dumfregia huxleyi.*

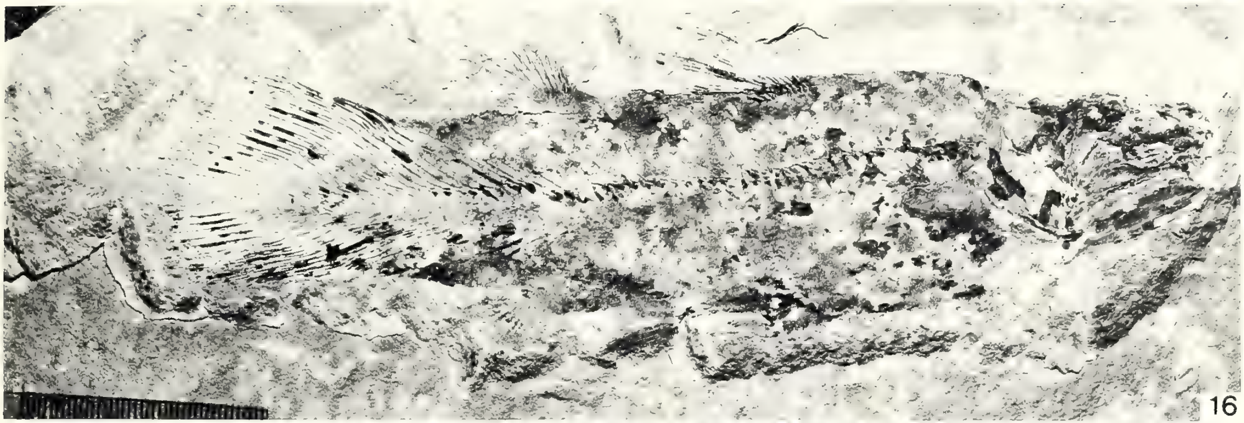
BEAR GULCH COELACANTHS

Family Rhabdodermatidae

Genus ***Caridosuctor*** Lund and Lund, 1984

Type species.—Caridosuctor populosum Lund and Lund, 1984.

Diagnosis.—Marine rhabdodermatids that differ from other genera in having large teeth on dentary, precoronoids, and ectopterygoid. Preorbital region higher and more rounded than in other members of the family, cheek bones deeply overlap each other and operculum, operculum articulates with tabular and posterior margin of the tabular level with posterior margin of skull. Ornamentation of tubercles



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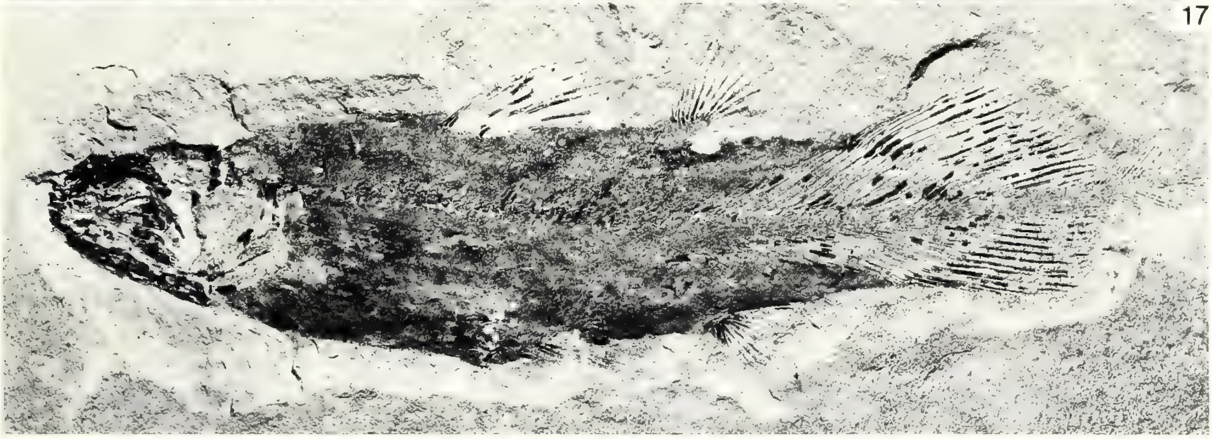

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Fig. 16.—*Caridosuctor populosum,* Type, MV 6021a. Scale in mm.
Fig. 17.—*Caridosuctor populosum,* Type, counterpart, MV 6021b.

sparse on skull roof and preorbital region, dense in large specimens on very thin cheek bones, and of dense vermiform ridges on operculum and angular of lower jaw posterior to angular pit line. First dorsal fin plate has ventral digitiform processes, second dorsal plate anteroposteriorly elongated and bears an articulation for the fin posteriorly, and anal plate, which rarely ossifies, a simple rod in ventral body wall anterior to first haemals. Pelvic plates very broad anteriorly, with three major and one minor anterior lateral processes.

Caridosuctor populosum Lund and Lund, 1984
Figs. 16–34

Previous reference.—"Long body," Lund et al., in press, Fig. 1.

Type specimen.—MV 6021.

Referred specimens.—MV 2557, 2804, 2917, 2924, 2928, 2997, 3092, 3567, 3570–3572, 3576, 3626, 3632, 3633, 3759–3761, 3820, 3861, 5547, 5548, 6022–6040, 6208–6214, 6939–6944, 7702. CM 25590, 27299–27306, 27309 (counterpart, 27311), 27310, 27312 (counterpart, 27313), 27314–27332, 30671–30710, 30717–30723, 35203, 35528–35536, 35675–35678, 37513–37519, 41067.

Horizon and locality.–Namurian A (E2B), Lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Diagnosis.—Coelacanth ranging from 30 mm to 217 mm in standard length, and of cylindrical body form. Caudal fin outline elliptical. Meristic characters are: Vert. segments, 9–11 cerv., 23–26 abd., 20–25 caud.; P^1, 13–15; P^2, 3–4+10–13; D^1, 3–4+7–9; D^2, 4–5+10–14; A, 2–3+10–13; caudal, dorsal rays, 3–4+14–16; caudal, ventral rays, 3–4+11–13. Proportional characters are given in Table 1.

Description.—The head length-standard length ratio describes a curve where the slope decreases markedly above about 120 mm in standard length, with very tight correlation (Fig. 20). Among meristic characters, variation in the number of precaudal segments is primarily related to coverage of the cer-

Table 1.—*Proportional statistics of* Caridosuctor populosum. *Abbreviations: Asp. R., aspect ratio of the caudal fin; GL/HL, gape length : head length; GL/LJL, Gape length : lower jaw length; GL/SL, Gape length : standard length; HL/SL, Head length : standard length; LJL/SL, lower jaw length : standard length; Max. ht./SL, Maximum body height : standard length; SD, standard deviation; Var., variance.*

Statistics	Max. ht. / SL	HL / SL	GL / HL	GL / SL	LJL / SL	GL / LJL	Asp. R.
Individuals over 100 mm							
N	15	13	13	14	14	14	12
Mean	.2256	.1596	.4894	.0784	.1565	.4936	.7989
SD	.0162	.0137	.0559	.0044	.0117	.0371	.0434
Var.	.0002	.0001	.0029	.00001	.0001	.0013	.0017
All pooled individuals							
N			16	17	16	17	
Mean			.4833	.0796	.1584	.4891	
SD			.0539	.006	.0135	.0352	
Var.			.0027	.00003	.00017	.00117	

vical series by the operculum and shoulder girdle, and becomes more marked with increasing size of the specimens. Variation in the number of caudal segments correlates directly with increasing size and consequent ossification of terminal elements. The taxonomic value of the meristic characters is limited, and will be discussed later in the paper. The taxonomic value of the proportional characteristics is very high in all Bear Gulch coelacanths.

The smallest known specimen, MV7702, is 30

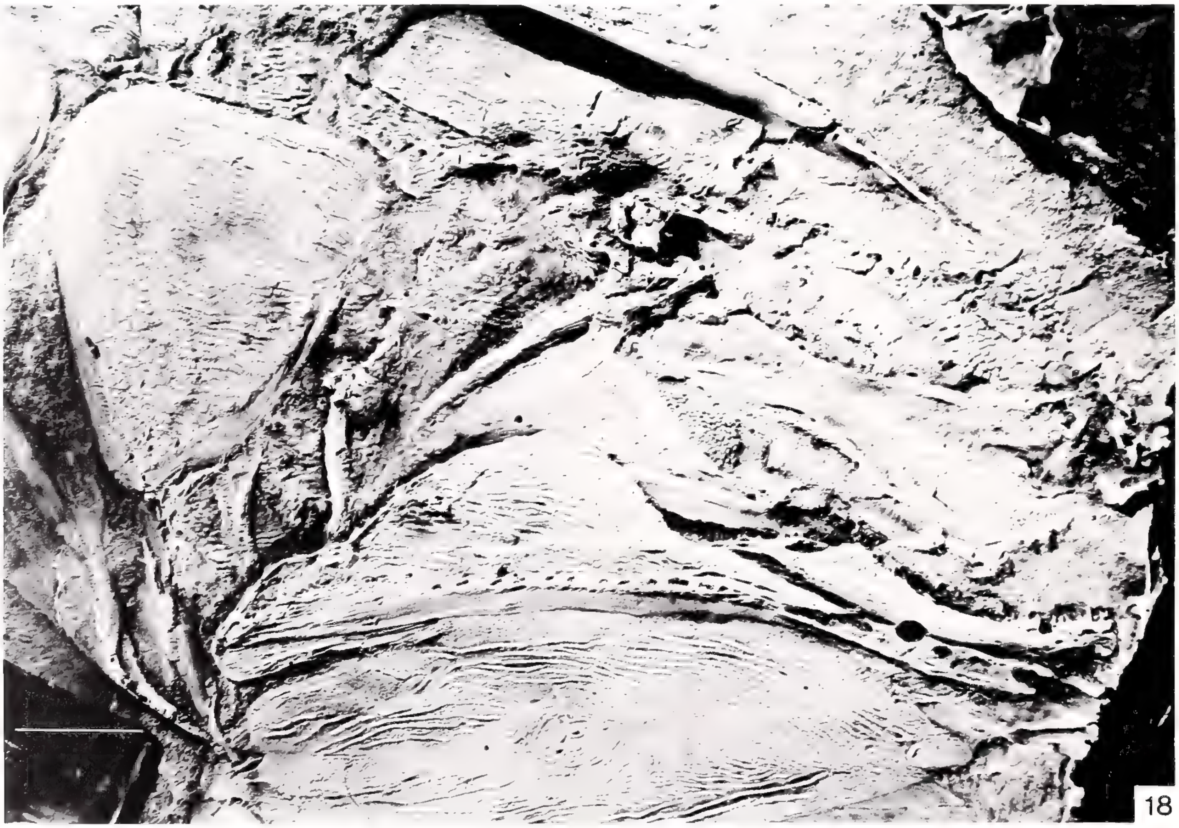

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Fig. 18.—*Caridosuctor populosum,* latex peel of head, CM 30723. Scale is 5 mm.

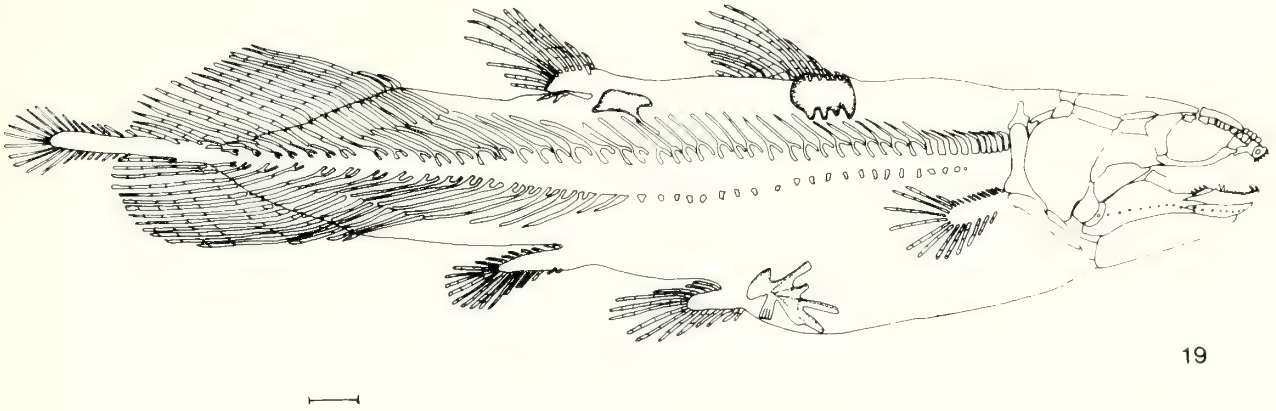

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Fig. 19.—*Caridosuctor populosum,* restoration, based on CM 25590, MV 6021. Scale is 1 cm.

mm in standard length and lacks scales. One other, very small individual is known, CM 41067, with scales, standard length of 42 mm. These two specimens have not been included in the statistics. There is one 55 mm individual, CM 30703. Specimens of 79 mm standard length and above are abundant. The size distribution of specimens strongly suggests that *C. populosum* may not have spawned in the sampled part of the Bear Gulch basin.

Ethmosphenoid region.—The premaxilla (Figs. 18, 21), as in *Rhabdoderma,* bears three to five large teeth, frequently with one of the tooth positions vacant. A large rostral pore perforates the ascending lamina. A small rostral bridges the gap between opposite premaxilla, followed by the anterior supraorbitals, then by a single postrostral. A single anterolateral rostral lies dorsal to the premaxilla and a large posterolateral rostral follows the premaxilla on the oral border. The contact between these two elements is minimal; at the posterior tip of the premaxilla, the anterior narial opening is located between them. The posterolateral rostral bears two or

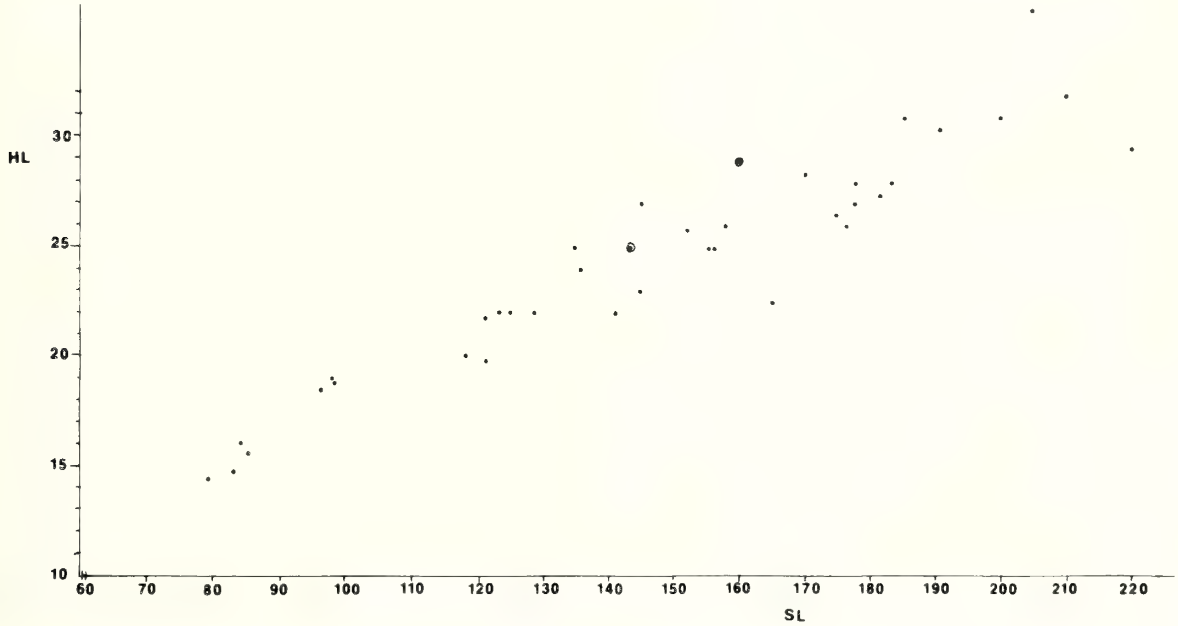

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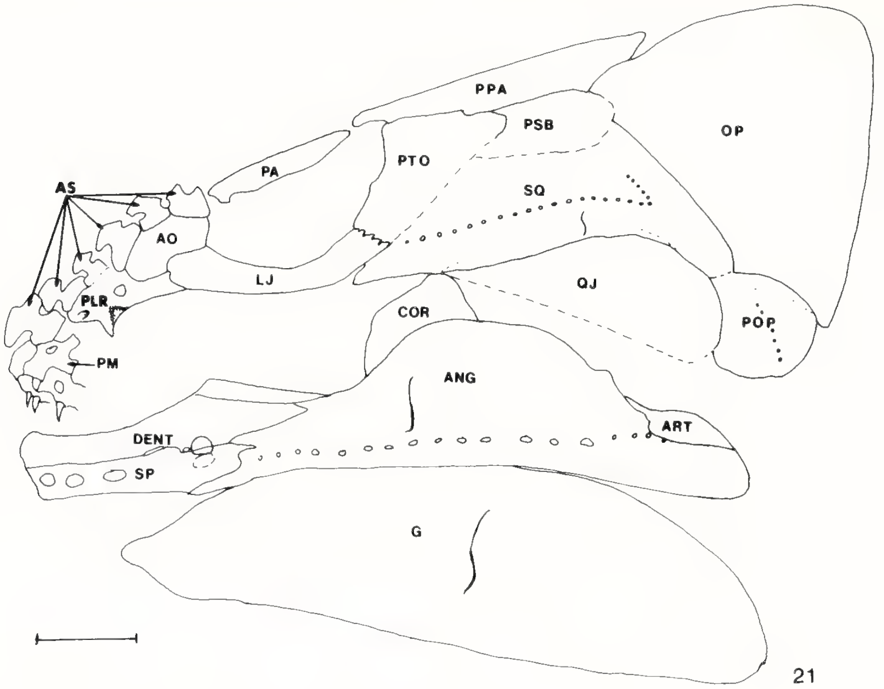
Fig. 20.—*Caridosuctor populosum,* graph of head length to standard length. Circled points = 2 specimens.



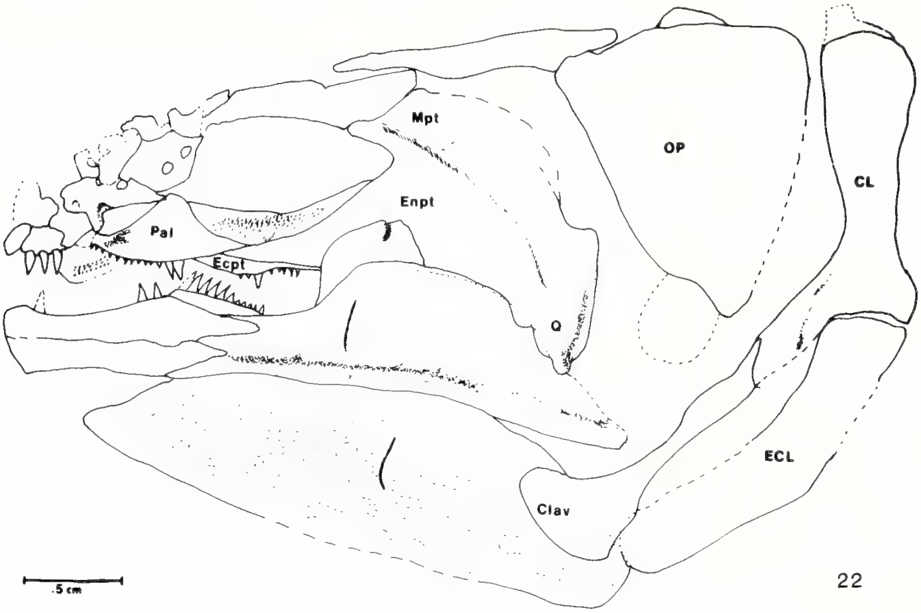
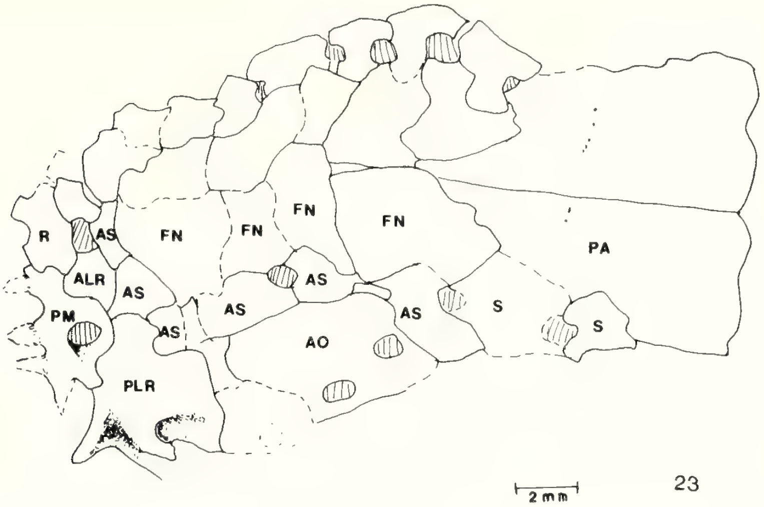


Fig. 21.—*Caridosuctor populosum,* dermal bones of the lateral surface of the head. From CM 25590. Scale is 1 cm. Abbreviations: AS, anterior supraorbitals; COR, coronoid; G, gular. Other abbreviations as in Fig. 4.

Fig. 22.—*Caridosuctor populosum,* deep view of left side of the head, based on CM25590. Scale is .5 cm. Abbreviations: CL, cleithrum; Clav, clavicle; ECL, extracleithrum; Ecpt, ectopterygoid; Enpt, endopterygoid; Mpt, metapterygoid; OP, operculum; Pal, autopalatine.

three infraorbital canal pores and a strong descending narial process, and probably forms the anterior border of the posterior nostril; a narrow posterior limb underlies the antorbital and contacts the lacrimojugal posteriorly (Fig. 21). The antorbital bears two large pores which are considered rostral organ pores.

There are seven anterior supraorbitals and seven



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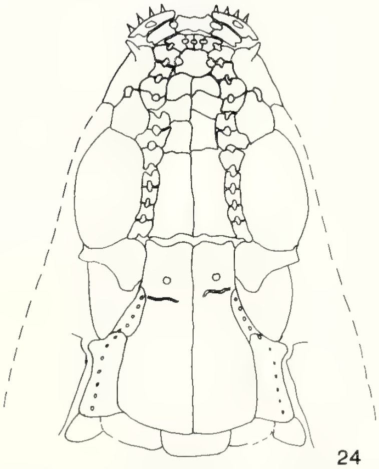

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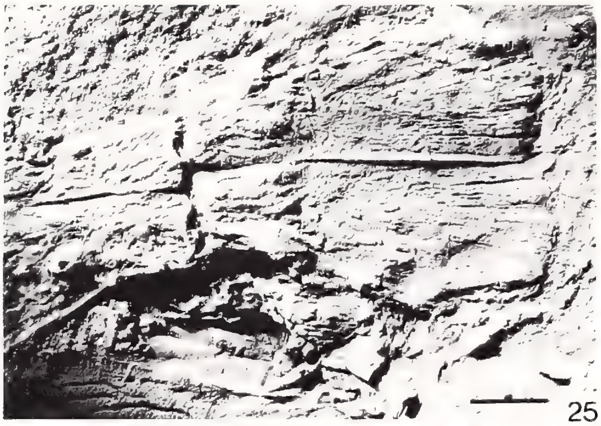
Fig. 23.—*Caridosuctor populosum,* skull roof of the ethmosphenoid moiety, CM 30681. Scale is 2 mm.
Fig. 24.—*Caridosuctor populosum,* restoration of the skull in dorsal view, based upon CM 30681.

supraorbitals over the orbit, the most posterior of which lacks a pore and lies behind the intracranial joint. The supraorbital canal pores are bordered principally by canal bones (Fig. 23), and not significantly by the frontonasal bones as in *R. elegans.* The degree of bone emargination by pores in the rostral region is minimal although the rostral, postrostral and premaxilla are emarginated and the precise shape of the anterolateral rostral cannot be determined. Of the above mentioned bones, only the more rearward of the anterior supraorbitals and the antorbital are ornamented with tubercles (Fig. 18).

There are generally four paired frontonasals anterior to the parietals, but asymmetry in numbers, size and shape of individual elements is common (Figs. 18, 23). The frontonasals are all thin elements, each of which tends to develop an area of central tuberculation relatively late in ontogeny. The parietals roof the orbital region, form the anterior edge of the intracranial joint, and are laterally scalloped for reception of the mesial edges of five supraorbitals. They bear a slight ethmoid lamina anteroventrally. The frontonasals appear to occasionally fuse with each other, and the parietals maintain a tight sutural contact across the midline except in the smallest individuals, in contrast to the loose connections in all *R. elegans.* The overall condition of the dermal bones of the preorbital region can best be described as loose, thin and flexibly joined.

Cheek.—The lacrimojugal is a thin, arcuate ele-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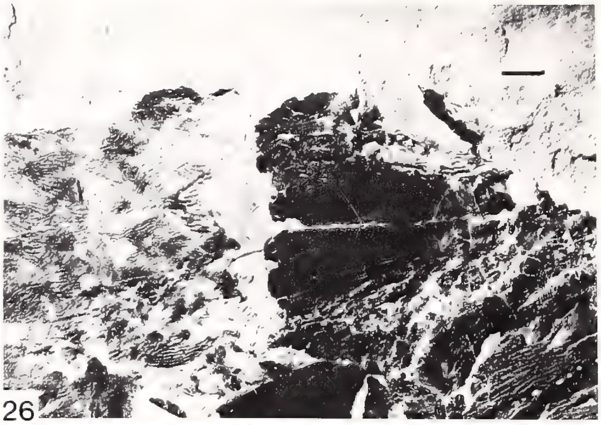
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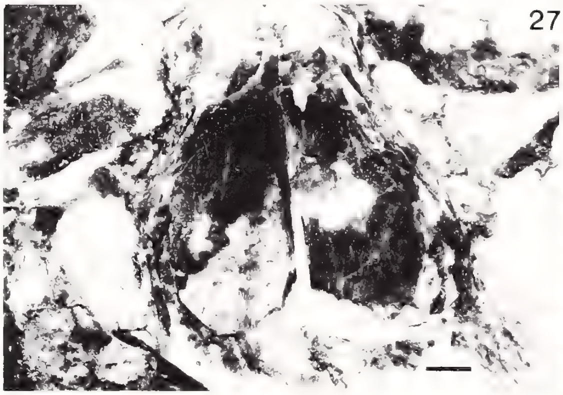
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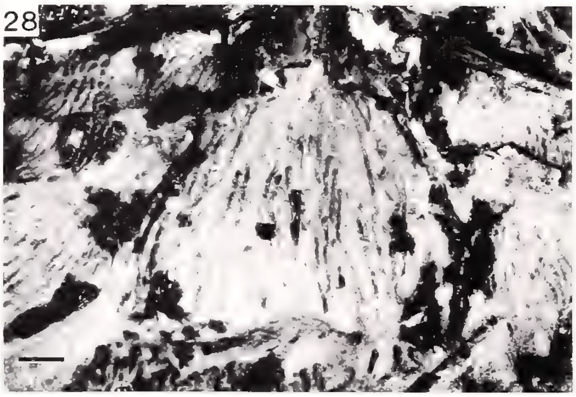
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Fig. 25.—*Caridosuctor populosum,* latex peel of the skull roof from the parietals to the rear margin, CM 30681. Scale is 2 mm.

Fig. 26.—*Caridosuctor populosum,* skull table of CM 27299b. Scale is 2 mm.

Fig. 27.—*Caridosuctor populosum,* skull table of CM 27305a, photographed under alcohol. Scale is 2 mm.

Fig. 28.—*Caridosuctor populosum,* skull table of CM 27305b (counterpart of Fig. 27), photographed under alcohol. Scale is 2 mm.

ment that is sutured with the antorbital and posterolateral rostral anteriorly and the postorbital posteriorly at the quadratojugal-squamosal junction. Pores are rarely evident in the lacrimojugal except at its anterior end. The postorbital is longer than high, its posterodorsal extension tapering to a point and overlapping the long, thin prespiracular. The anterodorsal corner of the postorbital adjoins the postparietal well behind the intracranial joint at the level of the posterior end of the posterolaterally projecting antotic process (Figs. 23, 24). The infraorbital canal, after receiving the horizontal (jugal) limb of the preopercular canal at the lacrimojugal-squamosal junction, traverses the postorbital to join the otic canal at the anterior end of the supratemporal, midway along the dorsal margin of the postorbital.

The quadratojugal, squamosal and preoperculum are thin bones with relatively closely set tubercular ornamentation (Fig. 18). The quadratojugal extends from the posterior edge of the coronoid process to the posterior edge of the quadrate. The preoperculum is overlapped by the quadratojugal anteriorly and overlaps the anterior edge of the operculum posteriorly. Both quadratojugal and preoperculum are overlapped by the squamosal, which also overlaps the operculum. A long, thin oval prespiracular extends from under the rear of the postorbital to fit against the tabular. The cheek bones are heavily ornamented but virtually lack a basal lamellar layer, resulting in preservation so poor that the paths of lateral line canals or pit lines can rarely be located. The preopercular canal emerges vertically into the squamosal and thereafter extends anteriorly, to the infraorbital canal. No large pores are present in the squamosal. The quadratojugal pit line extends vertically into the squamosal as a prominent groove. The operculum is the sole bone of the opercular flap. The anterodorsal corner of the operculum bears a

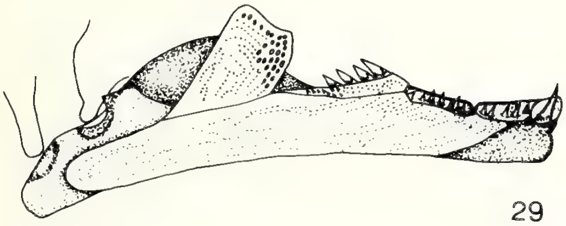


Fig. 29.—*Caridosuctor populosum,* restoration of internal view of the lower jaw, from CM 30723, 35530, MV 3567, 3761.

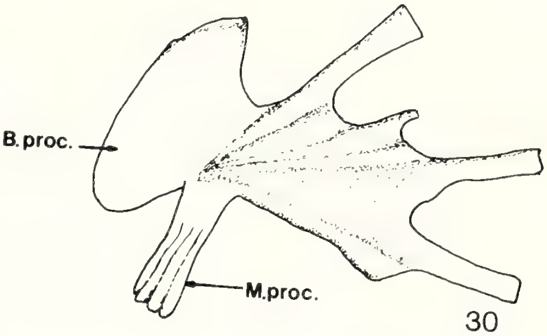


Fig. 30.—*Caridosuctor populosum,* pelvic girdle of CM 35203b. See Fig. 33.

well developed condyle and facet for articulation with the tabular (Fig. 18); the operculum projects considerably beyond the rear margin of the skull.

Oticooccipital.—The postparietal, the principal skull roofing bone of the oticooccipital part of the brain case, is bordered laterally by the narrow supratemporal and laterally expanded tabular (Figs. 24–28). The supraorbital canal cannot be seen to enter the postparietal, but can be seen to join the infraorbital canal above the postorbital (Figs. 25, 27). A pore and a faint lateral pit line are evident in the postparietal mesial to the anterior end of the supratemporal. The otic canal of the supratemporal continues into the tabular, opening to the surface by three large pores, and passes into the lateral extrascapular. There are five thin, scale-like bones in the extrascapular canal series, which carry the occipital commissure near their anterior edges.

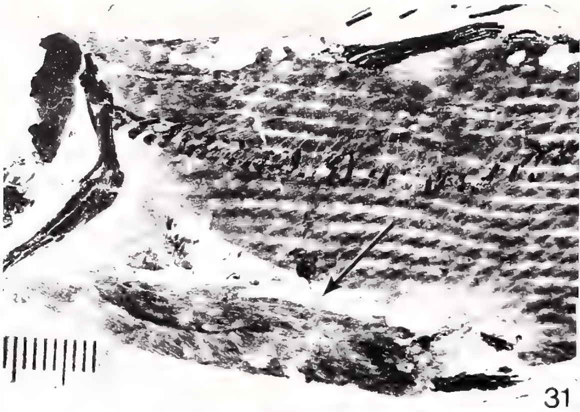
The otic canal in *Latimeria* receives only the infraorbital canal, and passes into the tabular in soft tissue lateral to the postparietal in precisely the position of the reduced supratemporal of the Rhabdodermatidae. The significance of the lateral line canal paths of coelacanths will be discussed later in this paper.

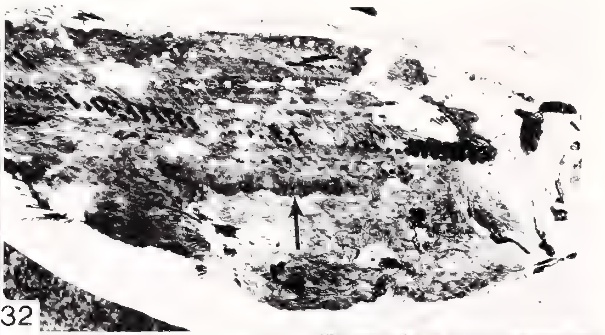
Palate, lower jaw, and branchials.—The shapes, proportions and relationships of the bones of the palate and lower jaw are very similar to those of other coelacanths.

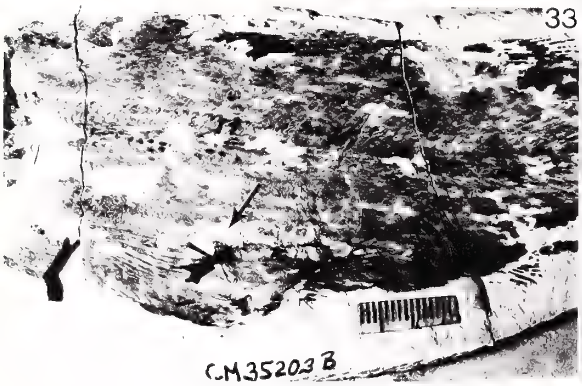
The triangular autopalatine is fringed with dermopalatine plates anteriorly and laterally, followed posteriorly by a long, thin ectopterygoid that extends to the level of the middle of the coronoid (Fig. 22). The dermopalatines and ectopterygoid bear prominent, finely striated teeth, whereas the endopterygoid bears posterodorsally oriented fine denticulated ridges. The metapterygoid is only loosely attached to the endopterygoid and does not bear teeth orally; however, a mosaic of tooth bearing plates lies mesial to the metapterygoid in the roof of the mouth and extends anteriorly to the middle of the orbit. The palate is very strongly curved outward near its posterior border.

The dentary and the underlying splenial, which carries the symphysial end of the mandibular lateral line canal, are relatively short, thin bones. The dentary bears only two or three large teeth near its posterior end. There is a long dorsal concavity or diastema in the dorsal margin of the angular anterior to the coronoid eminence (Fig. 18). The angular slopes gently posteroventrally from the coronoid to the lateral edge of the articular facet, exends horizontally briefly and then slopes strongly to the posteroventral corner of the lower jaw. The angular does not cover the retroarticular region of the articular laterally. The mandibular canal exits in the splenial and anterior angular through large pores, decreasing somewhat in size posterior to the vertical pit line. The mandibular canal pores curve dorsally at the articular. The lower jaw bears no ornamentation anterior to the angular.

There is a series of tooth bearing plates mesial to the oral border of the dentary; the parasymphysial plate bears one large tooth and many finer ones, whereas the more posterior plates bear a few moderate sized teeth grading into fine teeth. The precoronoid slopes posteroventrally to the base of the coronoid, and bears several large teeth along its dorsal rim as well as very fine teeth on its mesial surface (Figs. 22, 29). The quadrangular coronoid has a prominent saddle-shaped dorsal edge, articulates with the dorsal edge of the prearticular ventrally,







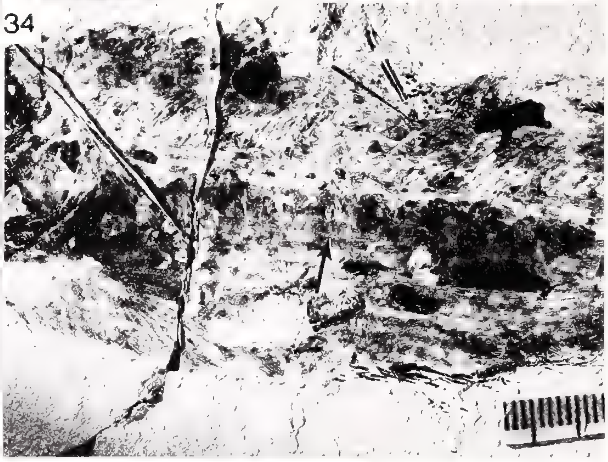


Fig. 31.—*Caridosuctor populosum,* CM 35675, midbody, scale in mm. Arrow points to intestinal filling.
Fig. 32.—*Caridosuctor populosum,* CM 35203a, same scale as Fig. 33. Arrow points to swim bladder.
Fig. 33.—*Caridosuctor populosum,* CM 35203b, scale in mm. Arrow points to fecal bolus.
Fig. 34.—*Caridosuctor populosum,* CM 35535, scale in mm. Arrow points to swim bladder.

and bears circumferential rows of rather blunt teeth anteriorly (Fig. 18) which become finer posteriorly and ventrally. In larger individuals the articular ossification is massive and includes the retroarticular region. In smaller individuals there is some reason to believe that there is a separate articular ossification for the quadrate condylar fossa anteriorly and ventrally, and a retroarticular ossification from the symplectic to the posterior corner of the jaw. The articular is most massive along the anterior wall of the fossa, and less massively ossified directly ventral to the quadrate.

Shoulder girdle.—The anocleithrum is a short element capping the cleithrum (Figs. 22, 31). There appears to be no direct bony contact with the braincase, again as in *Latimeria* (Millot and Anthony, 1958). The anocleithrum is rarely seen intact, however, and only the base is usually preserved. The cleithrum, clavicle and the extracleithrum show considerable ornamentation, but only in larger specimens. The clavicles meet in the ventral midline in a broad but very loose contact. The pectoral fin is borne at midflank, but while axial elements and the scapulocoracoid preserve as weak impressions they are never ossified.

Postcranial skeleton.—The first 9 to 11 neural arches are short, wide, and bear short spines inclined at a very low angle to the axis (Fig. 32). The angle of the succeeding three spines increases and the arches increase in height as they decrease in width (Fig. 19). The six neural spines underlying the first dorsal fin plate are of equal length, whereas those following the dorsal fin plate are noticeably longer except for the short neural spine bearing the second dorsal fin plate. The neural spines of the caudal region are longer than those of the thorax, each except the first three to four tightly associated with an epineural supporting a caudal fin ray. In most specimens the first epineural is free from attachment to a neural spine. Neural arches are borne upon all caudal neural spines. The arches approach a horizontal attitude posteriorly, whereas the spines and epineurals show increasing anterodorsally concave arching. Fin rays in turn are angled posteriorly from their bases of attachment to the epineurals, and are only articulated over their distal halves.

Strong rib bases are present on all thoracic vertebral segments, but there are no indications of ribs. Two incomplete haemals form the transition to the long posteriorly sweeping and anteroventrally concave haemal spines. The haemal arches and spines approach a horizontal attitude toward the posterior end of the column, the infrahaemals being straight elements descending from them at a pronounced angle.

The fin rays in the caudal lobe are unsupported by endoskeletal elements.

Peritoneal cavity.—An extensive, but thinly ossified and either coiled or partially partitioned (Figs. 32, 34) swim bladder occupies the dorsal portion of the gut cavity. The digestive tract itself is not infrequently preserved with phosphatic infilling or ingested food, and extends without evident curvature from the pharynx to immediately between the bases of the pelvic fins (Figs. 31–34). Traces of chitin and occasional scales can be seen in the intestinal filling of several specimens. Coprolitic masses occasionally can be found directly above the pelvic girdle; these never show spiral twists nor identifiable particulate matter on gross examination. A spiral valved intestine, however, is indicated by the impressions left by partially filled intestines, and by the straightness and extensibility of the digestive tract. The entire longitudinal extent of the peritoneal cavity of CM 27318, 150 mm in standard length, is occupied by an intact paleostomatopod shrimp *Tyrannophontes theridion* (Schram and Horner, 1978) 50 mm in length that lies head posteriorly. This is regarded as evidence that the intestine can be extended posteriorly from above the anus to the posterior wall of the peritoneal cavity, to accommodate large prey items.

Suborder Hadronectoroidei Lund and Lund 1984

Type family.—Hadronectoridae Lund and Lund, 1984.

Diagnosis.—Nasal-frontal-parietal series anamestic in early ontogeny flanked by mesial and lateral supraorbital canal series, and mesial canal series tends to fuse with nasal-frontal-parietal series during ontogeny. Supratemporal bone unreduced. Cheek of five bones, tightly fitted or overlapping. Opercular flap contains both opercular and subopercular bones. Postcranially, second dorsal fin axis articulates directly above its basal plate, anal fin plate directly below, and supported by, first haemal spines, and there is no extension of the peritoneal cavity posterior to the anus.

Included families.—Hadronectoridae, the only family presently known.

Family Hadronectoridae Lund and Lund, 1984

Type genus.—*Hadronector* Lund and Lund, 1984.

Diagnosis.—The same as for the suborder, only family.

Genus ***Hadronector*** Lund and Lund, 1984

Type species.—*Hadronector donbairdi* Lund and Lund, 1984.

Diagnosis.—Premaxilla bears a narrow dorsal lamina emarginated for one or more pores. Rostropostrostral series large, containing 6 bones and extending posteriorly to level of orbit. Lateral supraorbital bones fuse into 3 to 4 elements, mesial supraorbital bones very narrow over orbit. Large supratemporal contains anterior end of otic sensory canal and pores. Post temporal located behind lateral extrascapular. Postcranially, midabdominal, anteriorly forked, broad pelvic plates bear a posteromedian articular process. Caudal fin ray : radial ratio is 1:1.

Skull bones all heavily ornamented with closely spaced tubercles frequently anteroposteriorly elongated into short ridges on bones behind rostrum. Shoulder girdle ornamented with vertical ridges, and scales ornamented in a manner similar to the bones of head, except that some ornamentation may be convergent to rear of the scales.

Hadronector donbairdi Lund and Lund, 1984
Figs. 35–45

Previous reference.—"Short Stubby," Lund et al., in press, Fig. 1.—*Hadronector donbairdi*; Lund and Lund, 1984.

Type specimen.—MV 3635.

Referred specimens.—MV 3574 (counterpart, 3605), 3863 (counterpart, 3865), 5098, 6041, 6215. CM 27307, 27308, 30711–30713, 35537.

Horizon and locality.—Namurian A (E2B) lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group; south of Becket, Fergus County, Montana.

Diagnosis.—Short, stocky coelacanth, ranging in size from 28 mm to 108 mm. All external skull

Table 2.—*Proportional statistics of* Hadronector donbairdi. *Abbreviations as in Table 1.*

Statistics	Max. ht./SL	HL/SL	GL/HL	GL/SL	LJL/SL	GL/LJL	Asp. R.
N	8	8	6	6	6	5	5
Mean	.3508	.2062	.4708	.0957	.1869	.5187	1.1884
SD	.0368	.0131	.0683	.0075	.0044	.0487	.0719
Var.	.0012	.0001	.0039	.00004	.00001	.0019	.0041

bones are heavily ornamented, ornamentation not necessarily in concordance with underlying bone pattern. Premaxilla with heavily tuberculated dorsal lamina, tuberculations grading into fine teeth along ventral margin. Small extracleithrum present in shoulder girdle. Caudal fin outline almost square cut. Proportional characters in Table 2. Meristic characters are: vert. segments, 9 cerv., 13 abd., 19–24 (mean = 21.6) caud.; P^1, 11; P^2, 3+8; D^1, 3+11; D^2, 2–3 (mean = 2.75) + 7–11 (mean = 8.25); A, 3+7–9 (mean = 8); caudal, dorsal rays, 3–4 (mean = 3.14)+18–21 (mean = 19); caudal, ventral rays, 3–4 (mean = 3.28)+17–21 (mean = 18).

Description

Hadronector is the only Bear Gulch coelacanth for which a growth series cannot be adequately demonstrated. All specimens but one range from 19–21.7 mm in head length and from 93–108 mm in standard length, are well ossified throughout, and can be presumed to represent adult specimens. CM 35537, which is unscaled and unornamented, seems to conform closely in observable features and proportions with *H. donbairdi.* It has head length of 5.3 mm and a standard length of 28 mm, although the axis is somewhat disturbed. There are no intermediate stages, indicating that alone among the Bear Gulch coelacanths, birth and growth may have taken place elsewhere than in the environments we have quarried.

Ethmosphenoid.—The ethmosphenoid moiety of the skull roof is complex, and interpretation of it is made more difficult by several factors. There is a discordance between the patterns of bones seen in mesial view and the patterns of the bones produced by growth and fusion of odontodes forming the external ornamentation. There is a discordance between the large pores midway along the transverse borders between members of anteroposterior series as seen in mesial view, and the small external pores that are seen in external view. There is also clear anteroposterior fusion of the basal bones of some

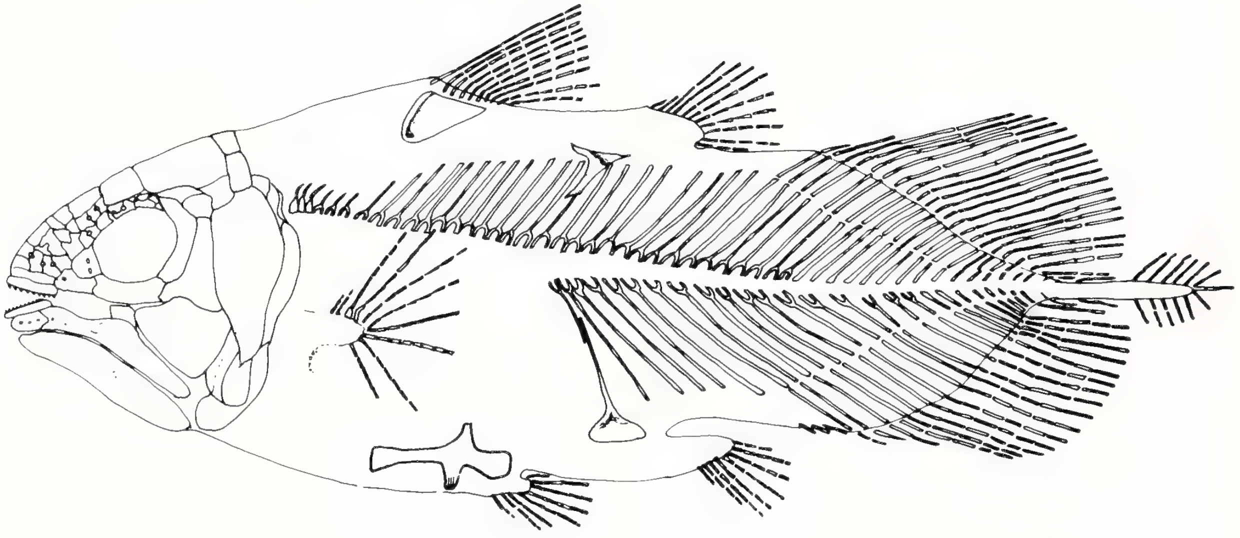


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Fig. 35.—*Hadronector donbairdi,* restoration based on MV 3635, CM 30723.

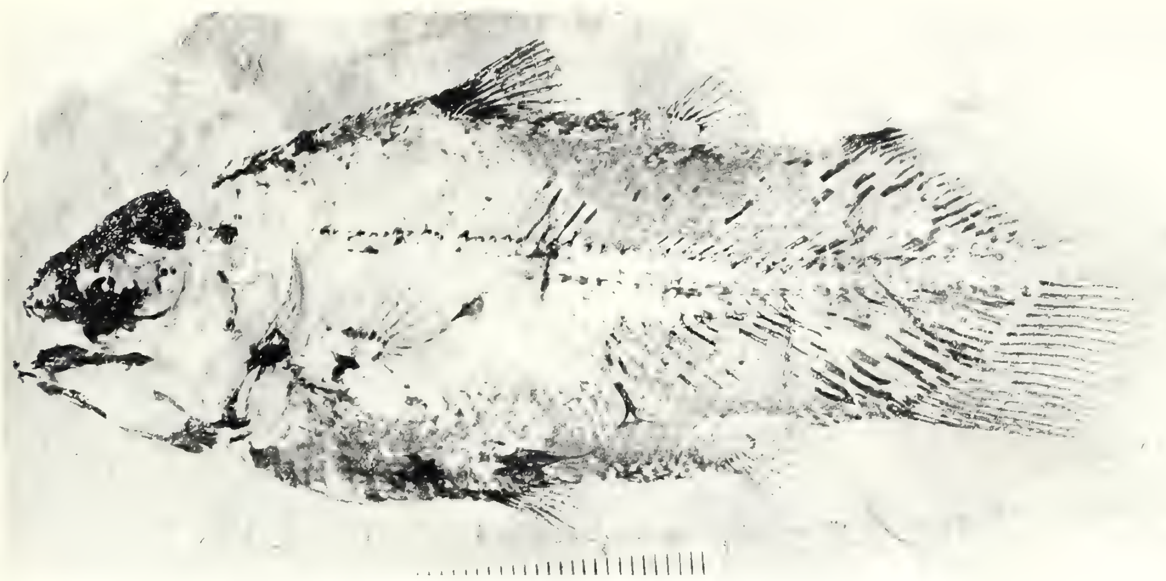

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Fig. 36.—*Hadronector donbairdi,* Type, MV 3635. Scale is 2 mm.

members of the supraorbital and frontonasal series, which varies somewhat among individuals. Finally benzene applied to bones, which usually reveals incremental growth lines, suggests that each anterior supraorbital bone may be a binary element. Indications of an overgrown suture can be found across the narrow isthmus bridging the lateral line canal between two originally polygonal elements.

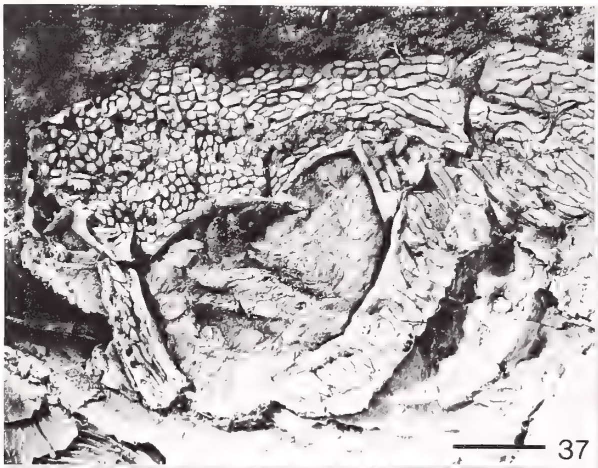
The premaxilla bears a low dorsal lamina ornamented with vertically oriented tubercles that grade into fine marginal teeth. The lamina is dorsally emarginated for two pores. Dorsally there appears to be a single anterolateral rostral. Neither premaxillae nor anterolateral rostrals meet in the midline.

The rostral series consists of six median elements, extends to the midorbital level, and is bordered posterolaterally by the parietals (Figs. 39, 42, 44). The ethmoid commissure traverses the most anterior bone of the series, the rostral. The frontonasal series, anterior to the parietals and lateral to the rostral series, is composed of six bones, one of which may be excluded from contact with a postrostral (Fig. 43). The most posterior element of this series is a product of either deep (bony) or superficial (odontode) fusion from two separate bones, and retains only marginal or near-marginal pores in superficial view. Lateral to the parietals the frontonasal series is posteriorly continuous with a series of eight small mesial supraorbital canal bones that extend back to the intracranial joint. There is particularly conspicuous discordance between the odontode layer and the mesial supraorbital series.

The lateral supraorbital series lies lateral to the frontonasal series anteriorly and the mesial supraorbital series posteriorly. The anterior elements each appear to have been binary elements earlier in ontogeny. There are 9 bones in the series from the rostral to the enlarged element forming the anterodorsal border of the orbit. Three lateral supraorbitals form the dorsal border of the orbit. The anterior of these is a simple bone but the posterior two are elongate and each may be product, by odontode growth and bone fusion, of four elements. There are no pores in either of the posterior two supraorbitals.

There is an additional series of three bones bordered by the anterolateral rostral anteriorly, the posterolateral rostral laterally, the antorbital posteriorly and the lateral supraorbital series mesially (Fig. 41). These bones are also notched for pores. This series is clearly shown in MV 3635 but is not evident in either CM 27307 or CM 30711 (Fig. 43).

In the infraorbital canal series, the lacrimojugal is an unusually stout element, heavily ornamented, and bears fine pores posteriorly grading into large pores near the anterior end of the bone (Figs. 37, 39, 40). Between the anterior end of the lacrimojugal and the supraorbital series lies the antorbital, perforated by one large pore without evident connection to any canal (Fig. 37). The posterolateral rostral is stout, with a prominent nasal prong anteroven-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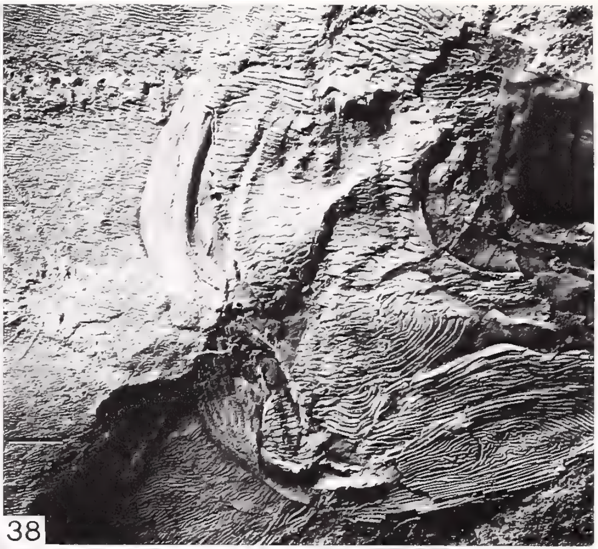
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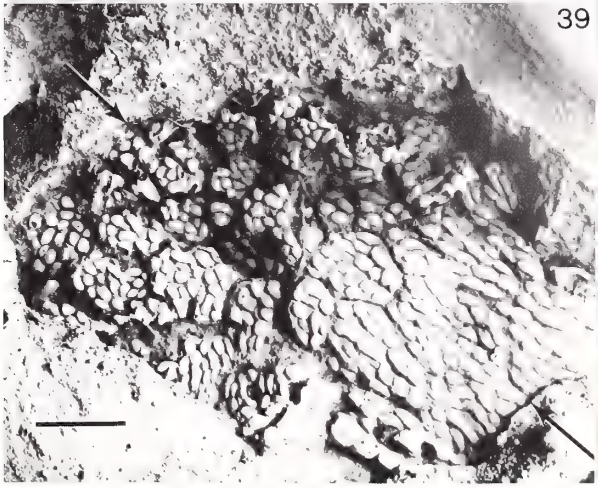
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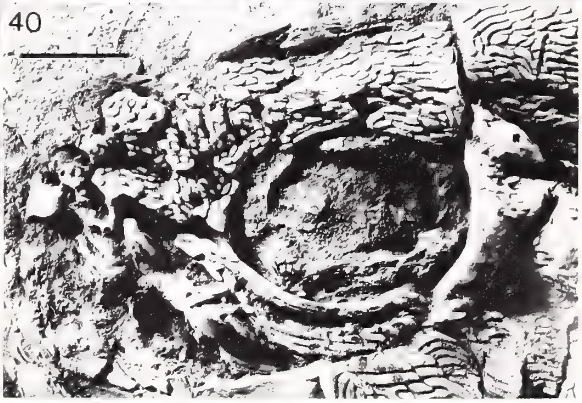
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Fig. 37.—*Hadronector donbairdi,* latex peel of the external bones of the ethmosphenoid moiety, MV 3635. Scale is 2 mm.

Fig. 38.—*Hadronector donbairdi,* latex peel of the posterolateral aspect of the head of CM 27307. Scale is 2 mm.

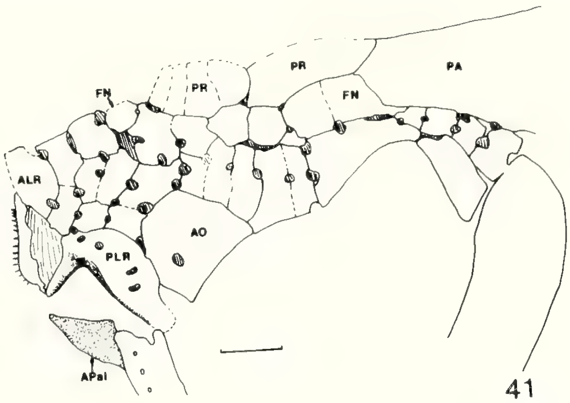
Fig. 39.—*Hadronector donbairdi,* latex peel of the middorsal aspect of the anterior ethmosphenoid moiety of MV 6215. Scale is 2 mm; arrows indicate dorsal midline.

Fig. 40.—*Hadronector donbairdi,* latex peel of the anterolateral aspect of the head of CM 27307a. Scale is 2 mm.

trally; the numbers of pores are not clear and their pathways through the bone may have been irregular. It is not possible to determine the number of elements involved in the anterolateral rostral area, although it appears to be one bone bordered anteriorly by the premaxilla. The premaxilla itself is emarginated dorsally for two pores, and these pores as well as the number of adjoining supraorbitals support the conclusion that three elements may have been involved in the formation of the anterolateral rostral.

Clear infillings of the lateral line canals of the ethmosphenoid region are absent in *Hadronector,* but traces of infillings and relationships of the pores make it possible to indicate the path of the canals with some confidence (Figs. 41–44). Pores of the supraorbital canal do not ever seem to perforate the bones except where clear secondary fusion has occurred, and preponderantly occur along transverse lines in sets of three (Figs. 39, 44). Pores of the infraorbital canal are large but irregularly developed anterior to the lacrimojugal, the canal underlying the lateral rostral series. The supraorbital canal evidently underlay the median supraorbital series above the orbit, and may have underlain the border between the frontonasal series and the lateral supraorbital series antorbitally. A commissure between supraorbital canals almost certainly was present between rostral series bone two and three (Fig. 43). There is evidence from pore distribution that a communicating canal exists between the supraorbital canal at the commissure and the infraorbital canal between the rostral and the anterolateral rostral (Fig. 44). There is no direct evidence on whether a separate ethmoid commissure existed at the rostral, as in *Allenypterus* (see below), *Acipenser* (Jarvik, 1948) and *Latimeria* (Millot and Anthony, 1958). It is believed, however, that the ethmoid commissure passes through the rostral, the communicating canal is the anterior lateral commissure, and the commissure between supraorbitals the antorbital commissure (Figs. 62, 75). There is no evidence in *Hadronector* for any association between the antorbital pore and any canal, nor is there any evidence for a posterior lateral commissure.

Cheek.—The cheek contains the usual compliment of postorbital, prespiracular, tall squamosal, quadratojugal and preoperculum, all but the prespiracular heavily ornamented, and tightly fit together (Figs. 40, 43). The infraorbital lateral line canal is joined by the jugal canal at the lacrimojugal-postorbital-squamosal boundary and is continued through the anterior margin of the postorbital. The anterior margin of the postorbital is level with the intracranial joint. Ornamentation of the postorbital is in the form of large posteriorly projecting serrations, and fine pores can be found between the bases of these serrations. The jugal canal is short and curves ventrally into the preopercular canal; no extension or pores occur dorsal to this junction although fine pores occur ventrally through the preoperculum. The quadratojugal pit line is prominent, extending from the dorsal half of that bone into the ventral aspect of the squamosal almost to the jugal canal (Fig. 40). The prespiracular is thin and appears flexible, and bears no trace of a canal. The suboperculum is much smaller than the operculum, and both bones are heavily ornamented.



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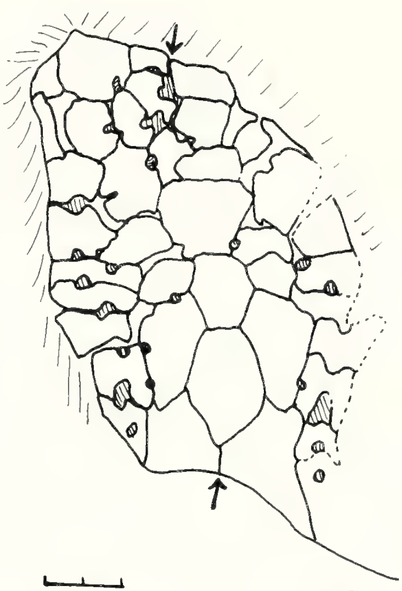

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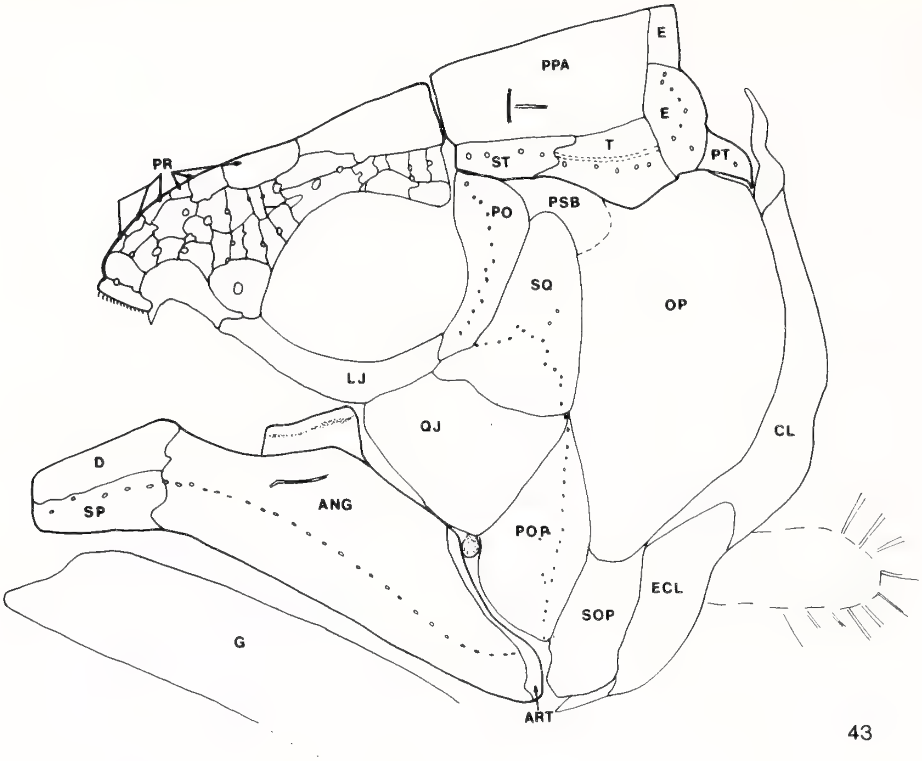
Fig. 41.—*Hadronector donbairdi,* reconstruction of bones of the snout of MV 3635. See Fig. 37.

Fig. 42.—*Hadronector donbairdi,* reconstruction of the bones of the middorsal aspect of the ethmosphenoid moiety of MV 6215. Scale is 2 mm. See Fig. 39.

Oticooccipital.—The oticooccipital moiety of the skull roof consists of large paired postparietals flanked laterally by moderate sized supratemporals and tabulars that gradually expand posterolaterally (Figs. 39, 43, 44). The posterior border of each supratemporal has a concave suture for the reception of the anterior end of the tabular. Three extrascapulars border the posterior margin of the skull roof. The infraorbital lateral line canal emerges from the anterodorsal end of the postorbital bone lateral to the anterior edge of the supratemporal. The otic canal continues through the supratemporal and tabular into the lateral extrascapular, where the supratemporal commissure branches off. Pores above the otic canal are few and large, whereas pores immediately posterior to the supratemporal canal are numerous and fine. T-shaped pit lines are usually prominent anterior to the middle of each postparietal, although the posterior pit line may be less prominent (Figs. 37, 38, 40). The anterolateral margin of the tabular forms the posterior wall of the spiracle.



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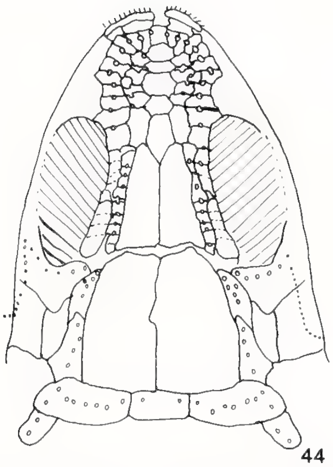

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Fig. 43.—*Hadronector donbairdi,* restoration of the external bones of the head in lateral view, based on MV 3635 and CM 27307.
Fig. 44.—*Hadronector donbairdi,* restoration of the external bones of the head in dorsal view, based on MV 6215 and 3635.

Palate, lower jaw, and branchials.—The anterior end of the palate is marked by a small but strongly ossified triangular autopalatine, faced ventrally with a toothbearing dermoplatine and anterolaterally by a fringe of small toothplates. There is a short ectopterygoid posteriorly (Fig. 45). The metapterygoid appears to be short and stout. Posteroventral to the extensive endopterygoid, the quadrate is strongly convex anterior to the articular condyle and ventral to the body of the endopterygoid. The palate is ornamented by concentric rings of fine denticles, the center being close to the quadrate (Fig. 45). The

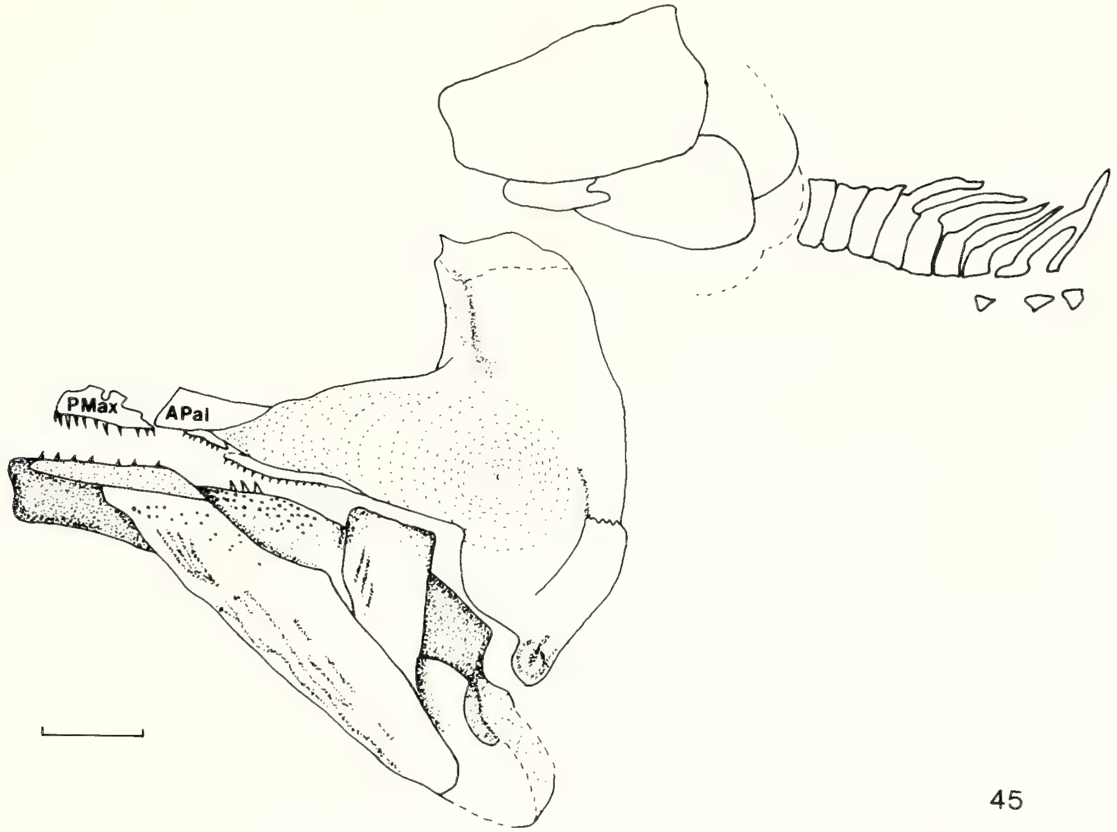

Fig. 45.—*Hadronector donbairdi,* internal view of the palate and lower jaw, with cervical neural arches. Based on MV 6041 and CM 27307. Scale is 3 mm. Abbreviations: APal, autopalatine; PMax, premaxilla.

palate articulates with the relatively short antotic process mesial to the anterodorsal edge of the postorbital bone. There is no evidence of a basipterygoid process.

The oral margin of the dentary and the associated splenial are oriented at a strong angle to the long axis of the lower jaw, and are quite short. There is a strong dorsal concavity at the anterior end of the angular before it rises to the coronoid eminence. At the posterior end of the angular, a distinct difference in ornamentation signifies that the posterior end of the ossification in Meckel's cartilage projects beyond the angular (Fig. 38). Large pores mark the course of the mandibular canal through the splenial and the anterior end of the angular, followed by fine pores posteriorly. The path of the pores of the mandibular canal curves dorsally below the articulation to meet the preopercular canal. There is a strong pit line in the angular immediately below the coronoid. The entire lateral aspect of the lower jaw is strongly ornamented (Fig. 38). The dentary bears a series of small teeth along its oral margin.

Mesial to the dentary can be seen a number of thin plates bearing small denticulations, extending over the anterodorsal end of the prearticular (Fig. 45). A large precoronoid extends to the coronoid, apparently abutting against it immediately mesial to the dorsal margin of the angular. The coronoid is quadrangular and sets upon the dorsal edge of the prearticular. The prearticular extends posteriorly to the level of the articular condylar fossa. Details of the retroarticular region are not preserved.

The branchial arches of *H. donbairdi* are unknown.

Shoulder girdle.—The postemporal is small, does not contact the tabular, and is closely associated with the anocleithrum-cleithrum contact. The anocleithrum bears a slightly S-shaped dorsal process. The cleithrum is long, with a short shaft connecting it to the relatively short clavicle, and the pectoral fin axis must have emerged somewhat lower on the flank of *Hadronector* than in any other Bear Gulch coelacanth (Fig. 40). The extracleithrum therefore, is also short, and is usually overlapped ventrally by the suboperculum. The cleithrum and extracleithrum are ornamented by strong, sharp vertical ridges.

Postcranial skeleton.—The first three postcranial neural arches are broadly in contact with each other and bear only slight median crests. The following four arches have successively shorter broad ventral extremities, and still lack significant neural spines. The eighth neural arch has a slightly broadened "footplate," and bears a short neural spine (Fig. 45), as do the succeeding two neurals. The following three neurals, under the first dorsal fin plate, increase in height posteriorly, and the remaining 10 neurals in the abdominal region are of normal height (Figs. 35, 38). The precaudal segments of *H. donbairdi* therefore consist of nine shortened, cervical neurals and only 13 abdominals. The stem of the second dorsal fin plate intercalates between the last two abdominal neural spines and bears an expanded, thin plate that is well ossified only along its ventral margin (Figs. 35, 36). The stem of the anal plate is supported below the first haemal spine and against the first full length haemal spine, and bears an anteroposteriorly elongated basal plate.

The pelvic plate resembles that of the rhabdodermatids and coelacanthids, bearing an anterolateral and anteromesial spur as well as a strong posterior median articulatory process interdigitating with the contralateral pelvic plate (Fig. 35).

An ossified swim bladder is present.

All median and paired fins are composed of well spaced and articulated fin rays, which are ornamented. Axial elements of the fins leave vague impressions, but were not ossified.

Genus ***Polyosteorhynchus*** Lund and Lund, 1984

Type species.—*Polyosteorhynchus simplex* Lund and Lund, 1984.

Diagnosis.—Dorsal margin of premaxilla emarginated for one or more pores and bears few, large teeth. Rostral bone small, postrostrals either very small or absent. Nasal-frontal-parietal series not bilaterally symmetrical and there are no enlarged, clearly defined "parietal" bones. Lateral and mesial supraorbital series unmodified by fusion. Anterior end of otic canal passes between postparietal and supratemporal. Anterior end of postorbital slightly behind intracranial joint, and squamosal may be present as one or two bones. Pelvic plates long, narrow, do not bear a posteromedian articular process, and are midabdominal. Caudal fin ray ratio is 1:1.

Polyosteorhynchus simplex Lund and Lund, 1984
Figs. 46–56

Previous reference.—"Big Head," Lund et al., in press, Fig. 1.—*Polyosteorhynchus simplex* Lund and Lund, 1984.

Type specimen.—MV 6043.

Referred specimens.—MV 2946, 3591, 6042. CM 27283, 30597, 30714, 35540.

Horizon and locality.—Namurian A (E2B), Lower Carboniferous Bear Gulch limestone member of the Heath Formation, Big Snowy Group; south of Becket, Fergus County, Montana.

Diagnosis.—Moderate sized coelacanth, ranging from 35 mm to an estimated 186 mm in standard length, and maximum height occurring midway between rear margin of head and origin of first dorsal fin. Bones of the skull relatively thin and ornamented with coarse, low, flat topped tubercles or ridges, although anterior bones of ethmosphenoid region sparsely ornamented and premaxilla devoid of ornamentation. Premaxilla bears 3–4 large teeth. Bones of cheek deeply overlapping. Extracleithrum large. Caudal fin outline almost square cut in larger specimens. Proportional characters given in Table 3. Meristic characters: vert. segments, 8–9 cerv., 23–24 abd., 25–26 caud.; P^1, 8–9; P^2, 12; D^1, 7; D^2, 14; A, 12–16; caudal, dorsal rays, 3–4+14–15; caudal, ventral rays, 3–4+14–16.

Description

Specimens of *P. simplex* are uncommon in the Bear Gulch coelacanth fauna, with only five complete measurable individuals. The largest, CM 30597, lacks a head but is complete from the rear margin of the operculum and shoulder girdle to the tip of the median caudal lobe; its length has been estimated on the basis of the proportions of the complete specimens (Fig. 73).

Two specimens, CM 35540 (Fig. 48) and MV 3591, measure 35 mm in standard length. CM 27283, with a middorsal skull length of 20 mm, is roughly estimated to be 86 mm in standard length. The specimens provide remarkably good information on morphological changes with growth. Ornamentation is not present on the smaller specimens, and is represented by few sparse tubercles on the postparietals and the parietal region and few, coarse ridges on the angular and gular of CM 27283 (Fig. 52). The angular of the two smallest specimens is very low relative to its height and the height of the coronoid bone, only approaching adult proportions in

Table 3.—*Proportional statistics of* Polyosteorhynchus simplex. *Abbreviations as in Table 1.*

Statistics	Max. ht./SL	HL/SL	GL/HL	GL/SL	LJL/SL	GL/LJL	Asp. R.
N	2	4	5	4	4	5	3
Mean	.3314	.2288	.3895	.0934	.1801	.5067	1.133
SD	—	.0165	.0905	.0184	.0333	.0609	.2309
Var.	—	.0002	.0065	.0002	.0008	.0029	.0355

CM 27283 (Figs. 5, 6). The outline of the caudal fin changes from elliptical in the small specimens to square cut by 105 mm (MV 6042) (Figs. 47, 48), and the median caudal lobe seems reduced to a virtual vestige at the largest size. As in all coelacanths reported on here, the number of caudal neural and haemal spines increases with absolute size as a result of increased ossification.

Ethmosphenoid.—The ethmosphenoid moiety of the skull roof consists of three paired series of small bones, the parieto-fronto-nasal series nearest the midline, and the mesial and lateral supraorbital canal bones (Figs. 50, 53). The bones normally termed parietals in coelacanths, namely the first paired elements anterior to the intracranial joint, that usually bridge the orbital region, are, in *Polyosteorhynchus,* produced by fusion during ontogeny of two bones in anteroposterior series. The anterior member, however, bears a strong anteroventral ethmoid lamina (Fig. 52). While there are usually five elements in the parieto-nasal series, the precise arrangement and proportions of these are variable from specimen to specimen as well as across the dorsal midline.

The mesial supraorbital series, consisting of 12 to 13 thin elements, evidently overlaid the supraorbital lateral line canal; each bone emarginated midway along the anterior and posterior borders for a large lateral line canal pore. The mesial supraorbital series of each side meets at the dorsal midline anterior to the parieto-nasal series in a manner strongly resembling the antorbital commissure of *Allenypterus* (Fig. 62) and *Hadronector* (Fig. 41). There are no clear indications of a median series of rostrals and postrostrals.

The lateral supraorbital series contains an element of uncertain shape overlying the antotic process and anterior to the dorsal end of the postorbital, continuous with the remainder of the series. From this element to the midpoint of the orbit, the bones of the series decrease in height and increase in width. Only two lateral supraorbitals occupy the anterodorsal corner of the orbit. The lateral supraorbital series continued as a series of seven to eight bones to the anterior part of the dorsal midline. The most anterior "orbital" supraorbital is bordered by the small antorbital ventrally and by a supplemental lateral ossification anteriorly (Fig. 53). This supplemental ossification (see *Allenypterus,* Fig. 60) overlays the antorbital-posterolateral rostral joint.

The infraorbital canal bones consist of the lacrimojugal, the posterolateral rostral and two or three anterolateral rostrals, bordered by the premaxilla

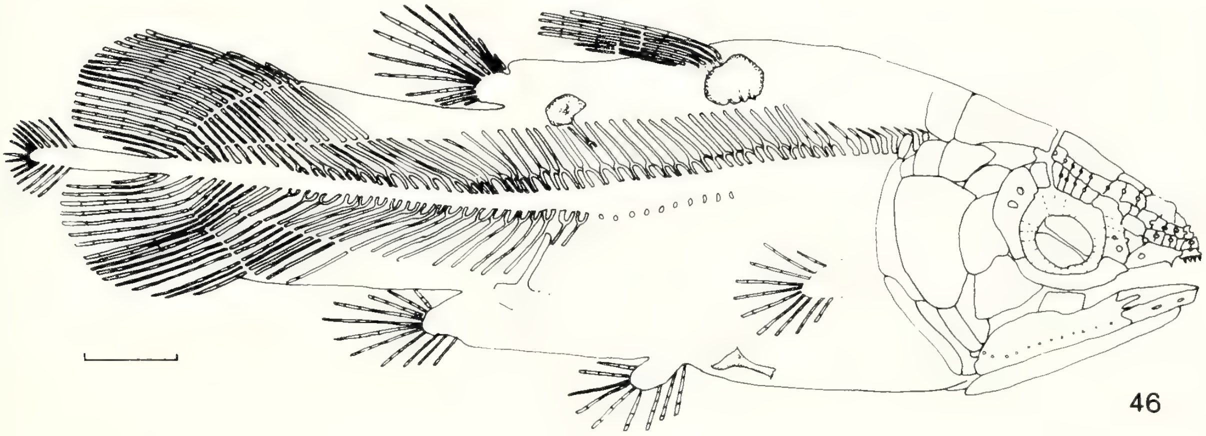

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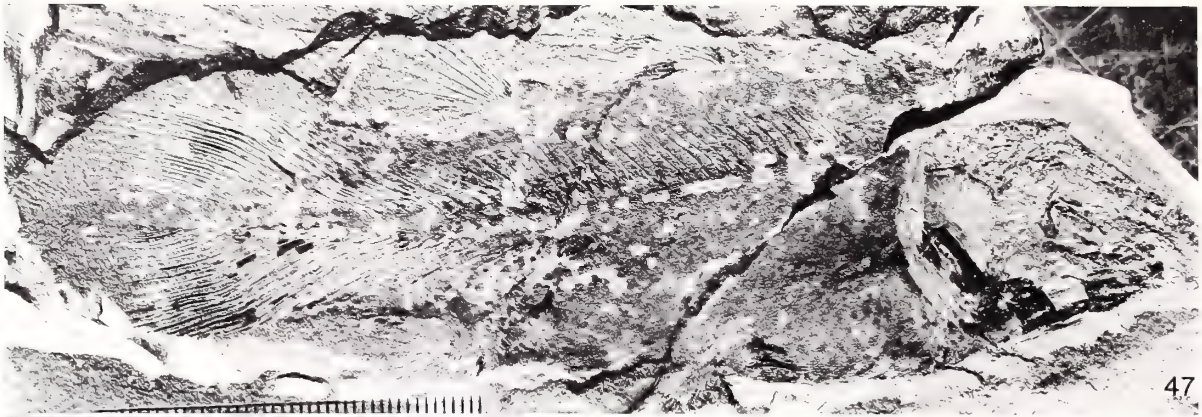
Fig. 46.—*Polyosteorhynchus simplex,* restoration based on MV 2946, 6042 and 6043.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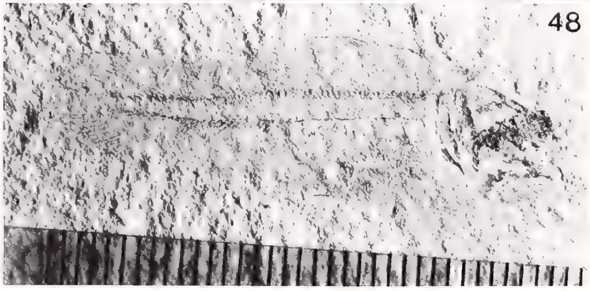
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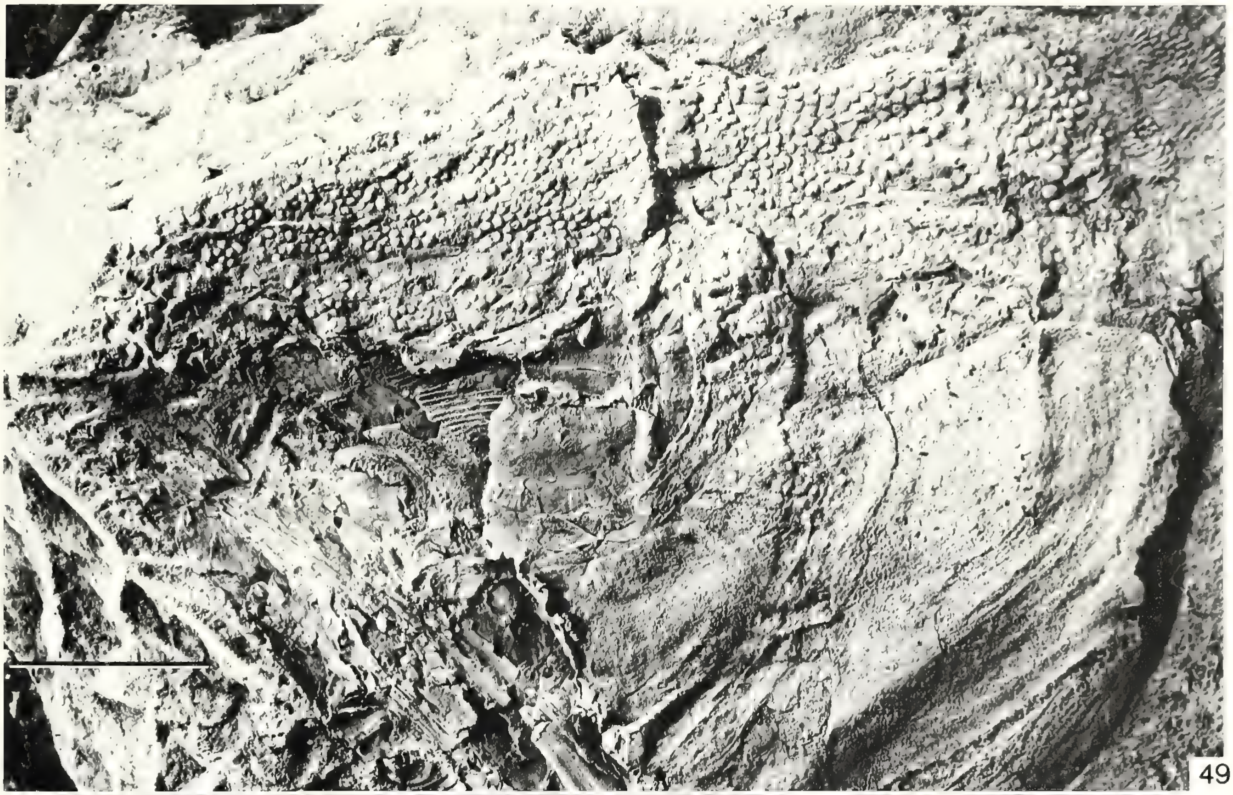
Fig. 47.—*Polyosteorhynchus simplex,* type, MV 6043. Scale in mm.
Fig. 48.—*Polyosteorhynchus simplex,* CM 35540. Scale in mm.

ventrally. The anterior pores of the infraorbital canal, or ethmoid commissure, are located between anterolateral rostrals and the premaxilla. There is a suggestion in CM 6042 of a very small element that could possibly be a median rostral.

The lateral line canal pattern of the ethmosphenoid moiety is essentially as in *Allenypterus montanus,* as far as can be determined from the few available specimens. There is clearly an antorbital commissure between supraorbital canals at the anterior end of the naso-fronto-parietal series, and most probably an anterior communicating canal between the canals at the anterior end of the lateral rostral series. There also appears to be a posterior lateral commissure between infraorbital and supraorbital canals, passing posterodorsally in front of the antorbital and either joining or ending in close proximity to the supraorbital canal at the most anterior "orbital" lateral supraorbital bone.

Cheek.—All bones of the cheek except for the postorbital are thin, heavily overlapping, and lightly ornamented with low pustules. The cheek bones except the postorbital also show circumferential growth lines of the basal lamellar layer, and most unusually, a central zone between the external ornamented zone and the lamellar basal bone. This highly textured zone is only typical of coelacanth and other sarcopterygian scales. A large quadratojugal bears scattered pits of the quadratojugal pit line and overlaps the tall, narrow preopercular enough to prevent accurate determination of the course of the preopercular canal. The preopercular canal in the squamosal rises to the vicinity of a large pit as in *Rhabdoderma elegans* (Fig. 6), and is met by the jugal canal ventral to the middle of the bone (Fig. 49). CM 6043, however, is conspicuously different from any other known coelacanth as well as other specimens of *P. simplex* in having a dorsal and ventral squamosal element. The ventral element carries the jugal and the ventral ramus of the preopercular canals, while the dorsal squamosal is, as far as can be determined, without either lateral line canal or pit line (Fig. 51). The significance of this difference is unclear, in view of the scarcity of specimens.

The operculum is tall, tapers ventrally, and is conspicuously ornamented in larger specimens with a concentric pattern of stout pustules (Fig. 51). It does not articulate directly with the tabular. The suboperculum is fitted around the ventral end of the operculum, is tall, narrower dorsally than ventrally,



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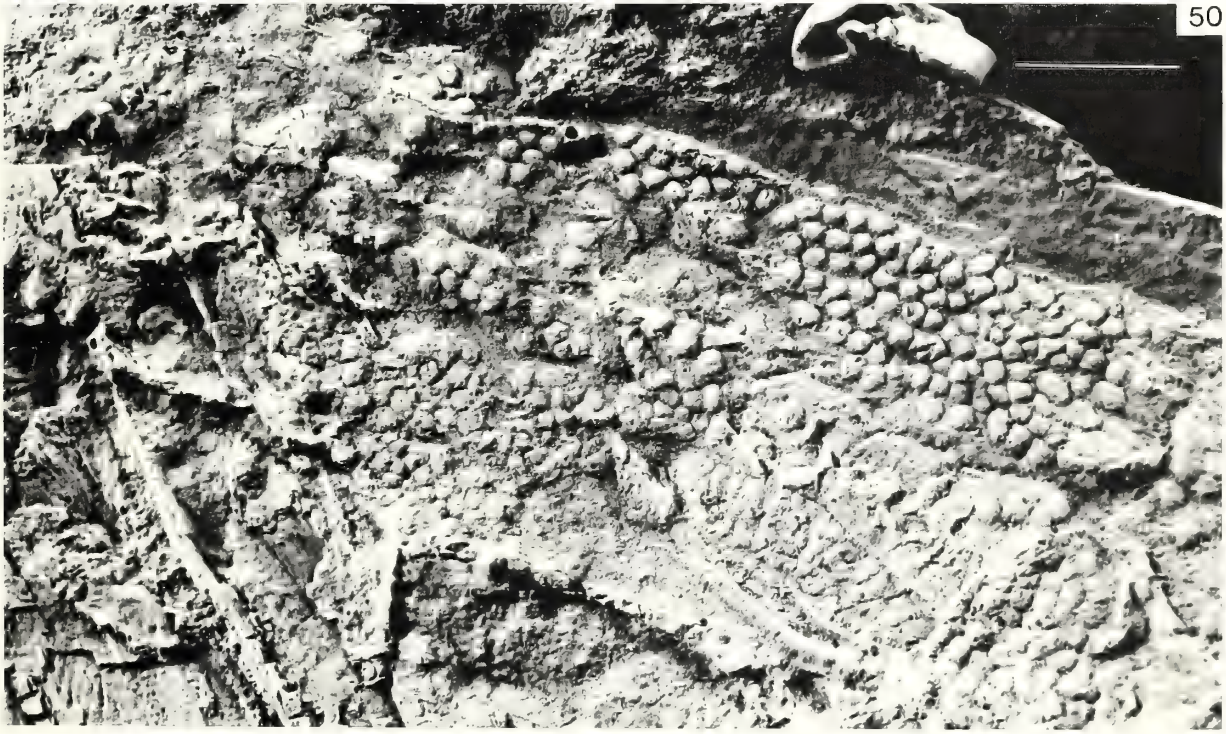

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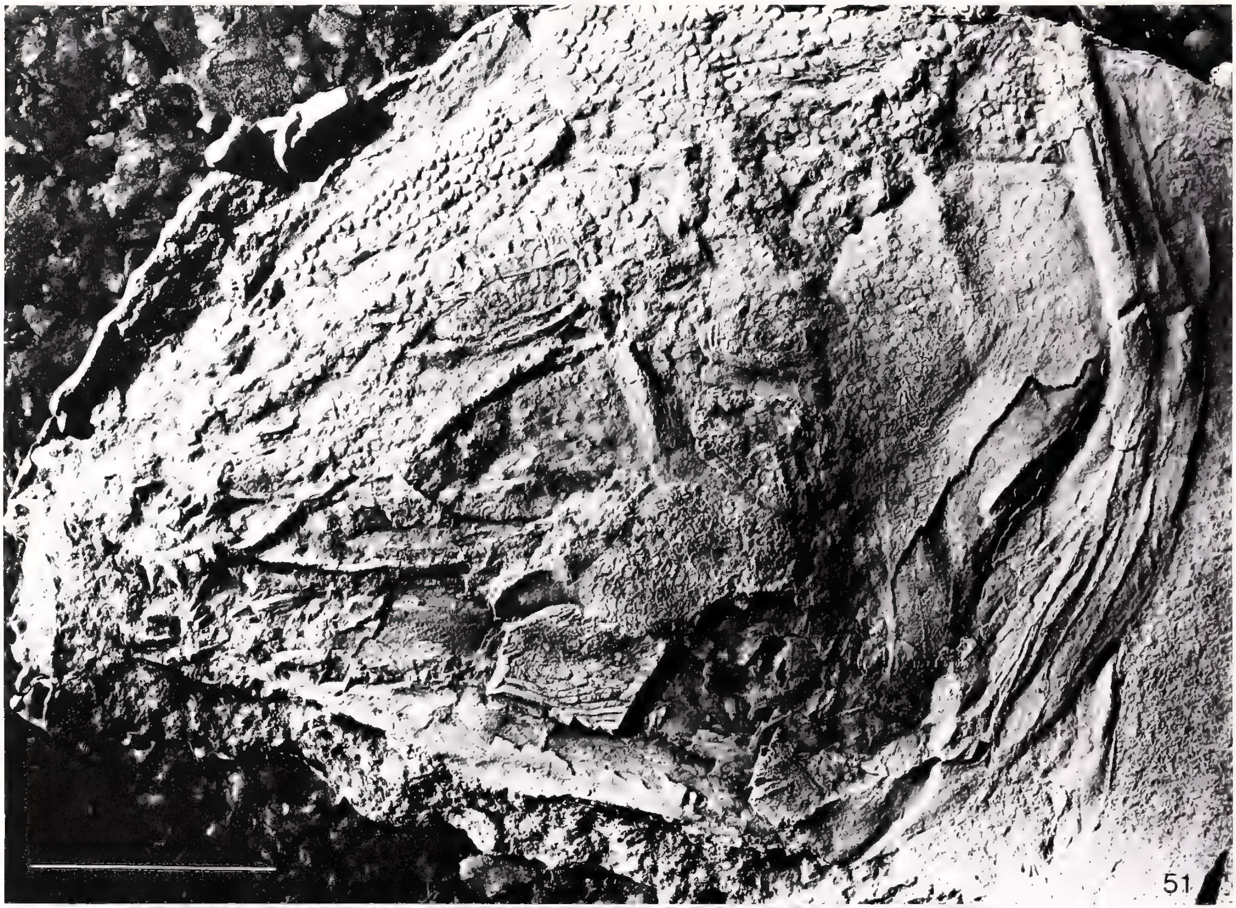
Fig. 49.—*Polyosteorhynchus simplex,* latex peel of the head of MV 6042. Scale is 5 mm.

Fig. 50—*Polyosteorhynchus simplex,* latex peel of the anterior part of the head of MV 6043. Scale is 2 mm.



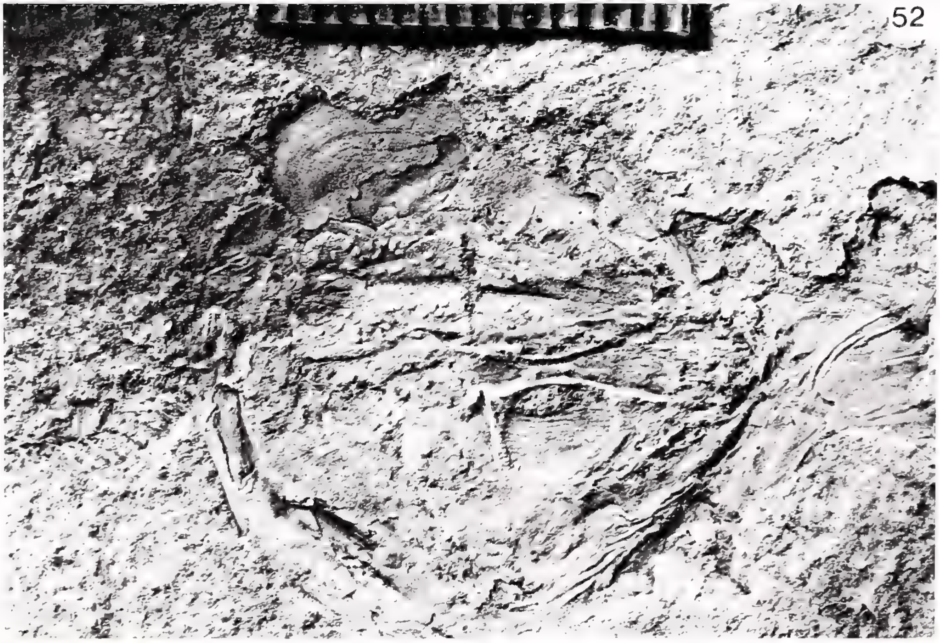


Fig. 51.—*Polyosteorhynchus simplex*, latex peel of the head of MV 6043. Scale is 5 mm.
Fig. 52.—*Polyosteorhynchus simplex*, latex peel of the head of CM 27283. Scale in mm.

and curves slightly forward under the posteroventral margin of the preoperculum. It is ornamented, as is the operculum, with stout pustules. The operculum and suboperculum are overlapped by the squamosal and preoperculum, and in turn usually completely overlap the shoulder girdle.

Oticooccipital.—The oticooccipital moiety of the skull roof consists of large postparietals flanked laterally by relatively wide supratemporals and tabulars and posteriorly by three extrascapulars (Fig. 49). There are no pores in the supratemporal; the otic canal passes between the anterior end of the supratemporal and the postparietal, leaving a prominent gap. The otic canal enters the tabular at its anteromesial contact with the supratemporal-postparietal suture and traverses the bone close to this suture, apparently giving off very fine pores. The anterolateral edge of the tabular forms a conspicuous, descending posterior wall of the spiracle, and there is reason to suspect that there is some fusion of this descending lamina with the posterolateral wall of the braincase (Fig. 49). An anterior pit line emerges onto the postparietal at the posterior end of the supratemporal gap (Fig. 49) and trends posteromesially. There is a space posterior to the end of this pit line, and a posterior pit line mesial to the rearward projection of the anterior pit line extends virtually to the posteromesial corner of the postparietal. There is some suggestion in CM 27283 of a lateral flange of the anterior end of the postparietal extending underneath the supratemporal and anterior part of the otic canal (Fig. 52). The postparietals are weakly joined in the midline.

Palate and lower jaw.—The palate is of typical coelacanth shape (Fig. 52) with an unusually wide metapterygoid region and stout epipterygoid process. A fringe of anterior dermopalatine teeth may be seen in front of the autopalatine. The ectopterygoid and the ventral edge of the endopterygoid to the quadrate bear few, relatively stout tubercles. The anterodorsal quadrant of the endopterygoid bears fine denticulated ridges, while the remainder of the endopterygoid and metapterygoid bear randomly oriented, fine denticulations (Fig. 49).

Few details of the lower jaw of *Polyosteorhynchus* are noteworthy, aside from the developmental information noted above (Fig. 56). The diastema of the jaw is small and relatively inconspicuous, rendered further so by the line of the precoronoid posterior to the end of the dentary. Many fine teeth on the anterolingual portion of the jaw seem to be borne upon a single plate. The prearticular is extensive, supports the coronoid, and bears longitudinal rows of denticulated ridges. The coronoid is quadrangular and seems to lack the prominent "saddle" seen in Rhabdodermatidae. There is a conspicuous projection of the lateral surface of the retroarticular posterior to the end of the angular, and there clearly are separate retroarticular and articular ossifications in CM 27283. These are not distinguishable in large specimens (Figs. 52, 56).

Although the smallest specimens show relatively well ossified gill arches, no details can be resolved aside from the observation that the branchial skeleton is not obviously different than that of other coelacanths from the Bear Gulch limestone.

Shoulder girdle.—The anocleithrum bears a stout spike-like vertical process, and seems to be tightly associated with the posttemporal (Fig. 51). The dorsal portion of the cleithrum is relatively short, weakly ornamented with vertical ridges, and bears a long anteroventral process articulating with the long dorsal arm of the clavicle. The clavicles are loosely associated in the ventral midline. The ventral ends of the clavicles are sturdily ossified and expanded. The extracleithrum is extensive and heavily ornamented. The articular process of the scapulocoracoid is ossified and projects beyond the extracleithrum-cleithrum junction but details cannot be resolved (Fig. 51).

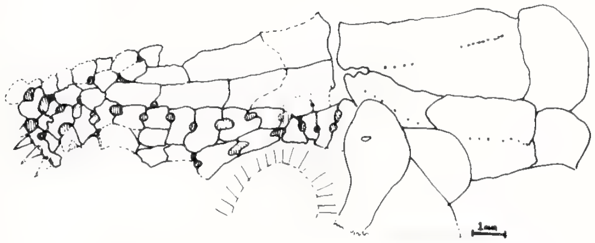
Postcranial skeleton.—An ossified swim bladder is present, as in every well preserved coelacanth.

The anterior seven to eight neural arches have laterally expanded bases; the first three bear only slight median crests. The following four to five arches bear strongly inclined, short neural spines. Postcranial neural arches nine and ten assume the narrow lateral aspect typical of those that follow while having neural spines inclined at the same angle to the vertical as the following abdominal arches. These spines are short, however. The succeeding four neural spines underlie the first dorsal fin plate and are slightly shorter than those of the remainder of the column (Fig. 46).

The pelvic plates are small, elongate and thinly ossified, without medial articulatory processes. The pelvic plates of CM 30597 are proportionately considerably longer than in MV 6043, but show no additional details.

Genus ***Allenypterus*** Melton, 1969

Type species.—*Allenypterus montanus* Melton, 1969.



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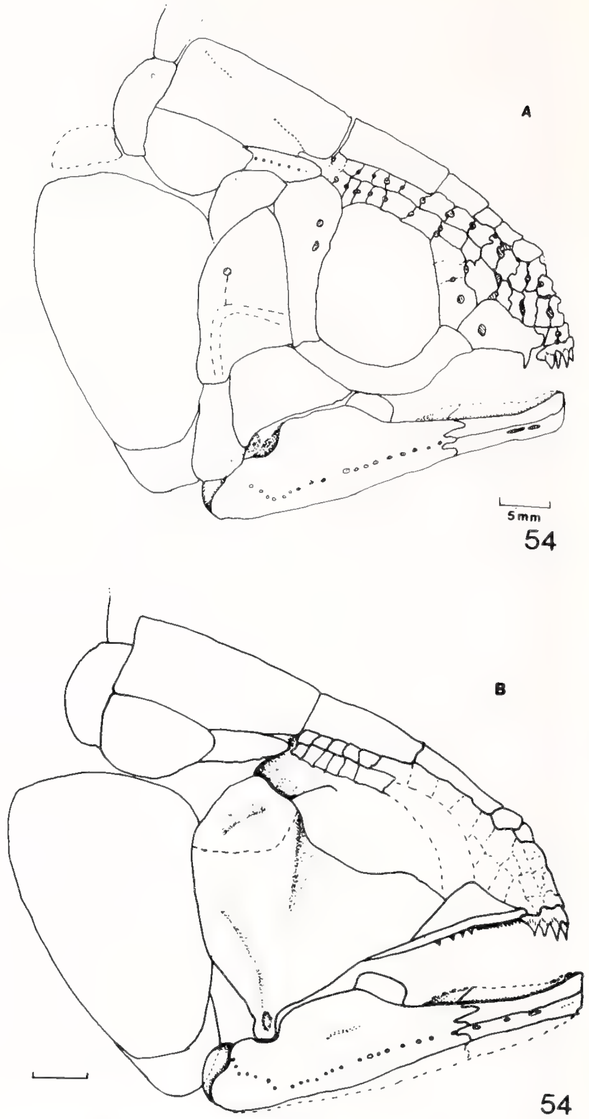

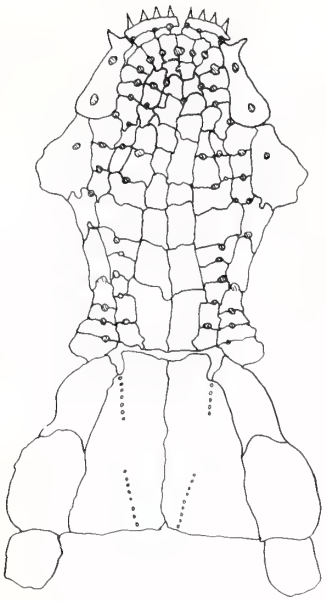

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Fig. 53.—*Polyosteorhynchus simplex,* reconstruction of the bones of the ethmosphenoid moiety of MV 6043. See Fig. 50.

Fig. 54.—*Polyosteorhynchus simplex,* A, restoration of the lateral view of the head, based on MV 2946, 6042, 6043; B, restoration of the palate, based on MV 2946, 6042, CM 27283.

Fig. 55.—*Polyosteorhynchus simplex,* restoration of the skull in dorsal view, based on MV 6042, 6043, CM 27283.

Revised diagnosis.—Premaxilla narrow, apparently unperforated and unemarginated, and bears a row of fine teeth. Median rostral and one postrostral both small and rostral possibly a fusion product. Mesial supraorbital series overlies lateral line canal and fuses relatively late in ontogeny with mesial skull bone series, resulting in a pored and canal bearing nasal-frontal-parietal series and an unmodified lateral supraorbital series. Several supplementary canal bones present between anterior supraorbital canal series dorsally and lateral rostral bones ventrally. Anterior end of otic canal passes beneath postparietal-supratemporal suture. Posttemporal in contact with posterolaterally expanded tabular. A median ventral row of thick scales between clavicles and pelvic girdle. Pelvic plates are high triangles that do not articulate in the ventral midline, and are located near rear of peritoneal cavity. Dorsal lobe of caudal fin originates anterior to level of first caudal segment, is elongate and has a fin ray : endoskeletal support ratio greater than 1:1. Fin rays and length of the ventral caudal lobe greatly reduced and have a 2:1 ratio to endoskeletal supports. "Median" caudal lobe bears no terminal fin rays.

Discussion.—*Allenypterus montanus* was originally described (Melton, 1969) as an actinopterygian of the family Dorypteridae. In all characteristics of cranial and postcranial morphology, except for the body form, *A. montanus* is clearly a coelacanth. The body form is unique among known coelacanths.

Allenypterus montanus Melton
Figs. 57–66

Previous references.—*A. montanus* Melton, 1969.
A. montanus, Glickman, 1977.
A. montanus, Lund et al. (in press).
A. montanus, Lund and Lund, 1984.

Type specimen.—MV 2555.

Referred specimens.—CM 27284–27288, 30627, 30628, 30716, 35200, 35202, 35363, 35538, 35539, 37509. MV 2771, 2920, 2949, 3640, 4736, 5381, 5382, 5549, 5550, 6216, 6217, 6937, 6938.

Horizon and locality.—Namurian A (E2B) Lower Carboniferous Bear Gulch Limestone member of the Heath Formation. Big Snowy Group, south of Becket, Fergus County, Montana.

Revised diagnosis.—Highly compressed, dacriform coelacanth with extended epichordal caudal fin and reduced hypochordal caudal. Body maximum height at origin of first dorsal fin, slopes downward from second dorsal fin to short, rayless median lobe. Epichordal caudal extends from close behind second dorsal to start of median lobe as series of short well articulated rays of uniform height. Size range from 32 mm to 152 mm standard length. All external bones of skull heavily ornamented with broad, flat topped ridges except premaxilla. Seven lateral supraorbitals over orbit, the most posterior two of which fuse, and five antorbitally. Bones of cheek thin, deeply overlapping each other, opercular series and rear of lower jaw. Meristic characters: vert. segments, 8 cerv., 20–21 abd., 36–44 caud.; P^1, 6–7; P^2, 6–7; D^1, 2–3+11–14; D^2, 6–9; A, 6–7; caudal, dorsal rays, 3–4+55–69; caudal, ventral rays, 15. 6–9 scales in median ventral scale shield. Proportional characters given in Table 4.

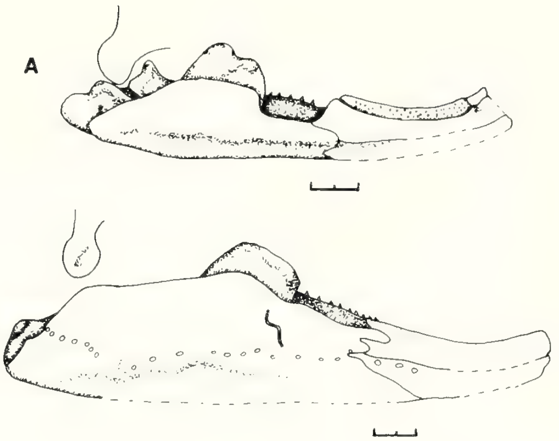

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Fig. 56.—*Polyosteorhynchus simplex,* lower jaws. A, from CM 27283; B, based on MV 2946. Scale is 2 mm.

Description

The body shape of *A. montanus* is unique among known coelacanths (Fig. 57). All other known coelacanths are approximately round in transverse section and relatively uniform in body height from the rear of the skull to the origin of the diphycercal tail. *A. montanus* is strongly compressed, with a short, high head and trunk, long asymmetrical tail with a dominant epichordal lobe, and a straight ventral outline. The median caudal lobe characteristic of coelacanths lacks a terminal tuft of fin rays and is rarely preserved; most specimens appear to have had the terminal bitten off, approximately at the level of the last few epichordal rays. Only four specimens are complete (Fig. 58). The smallest individuals show little of the dacriform outline of the adults; growth parameters are best fit by straight lines and maximum height increases most sharply in relation

Table 4.—*Proportional statistics of* Allenypterus montanus. *Abbreviations as in Table 1.*

Statistics	Max. ht./SL	HL/SL	GL/HL	GL/SL	LJL/SL	GL/LJL
N	11	11	4	4	4	4
Mean	.3598	.1874	.3598	.0666	.1434	.4567
SD	.0382	.0161	.0356	.0078	.0093	.0259
Var.	.0013	.0002	.0009	.0004	.00006	.0005

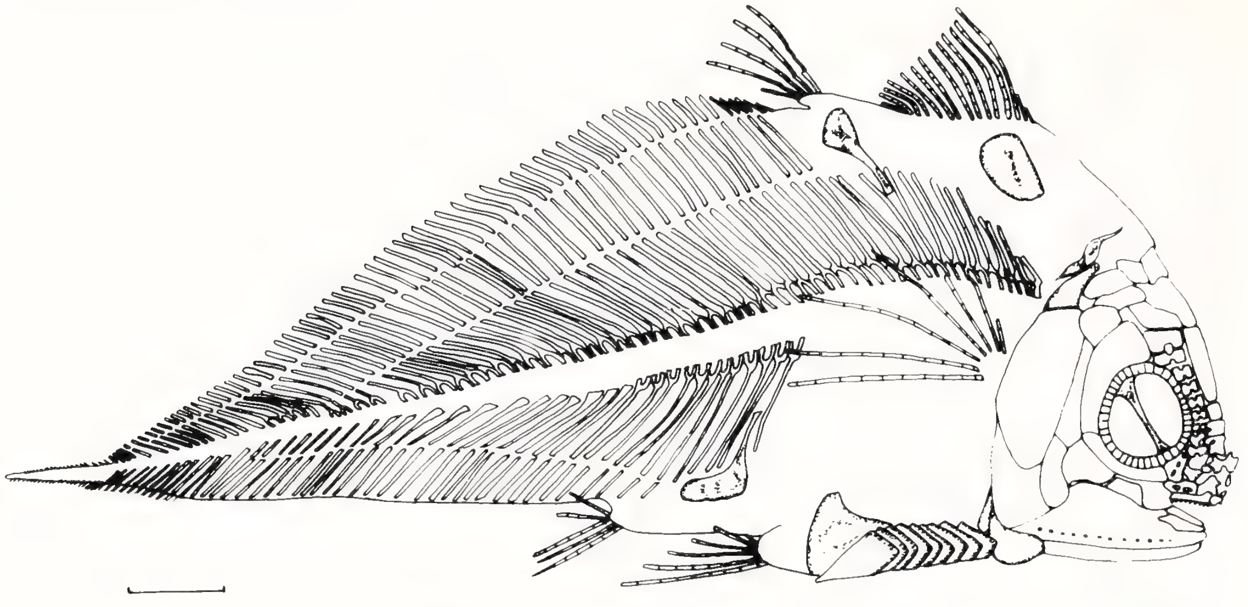

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Fig. 57.—*Allenypterus montanus,* restoration based on MV 5381, CM 37509. Scale is 1 cm.

to linear parameters around the head (Fig. 58). Linear parameters of head length to body length are virtually identical in slope to those of the other accurately measureable coelacanths in the Bear Gulch limestone (Fig. 72).

Ethmosphenoid.—The ethmosphenoid moiety of the skull roof of the largest individuals consists of a median rostral separated in the midline from a median postrostral, three to four paired frontonasals often asymmetrical and often accompanied by a peripheral frontonasal (Fig. 61), paired parietals, and a lateral supraorbital series, all of which are ornamented with anteroposteriorly oriented but basically circumferential flat topped ridges (Fig. 65). The nasal-frontal-parietal series bears pores that correspond with the marginal pores laterally in the supraorbital series. Pores of the supraorbital canal in the largest individuals tend to be subdivided anteroposteriorly and in places to be isolated from the margins of the bones, evidently by late growth of bone or ornamentation (Figs. 65, 66). Specimens of somewhat smaller size, such as CM 30627, and internal views of larger individuals usually reveal the calcite filled supraorbital canal in a wide space between the pore-free parietals and the well formed lateral supraorbitals (Fig. 64). Ossifications dorsal to the supraorbital canal are present, and are clearly similar to the supraorbital series in MV 6216. It can only be concluded that the bones of the nasal-frontal-parietal series of adults are each the result of the fusion of mesial supraorbital canal bones with the anamestic bones more mesiad. Thus the position of each pore in the parietals, the frontonasals, the most posterior, lateral supraorbital and possibly even the rostral, may mark the former location of a transverse suture between two elements (Fig. 61).

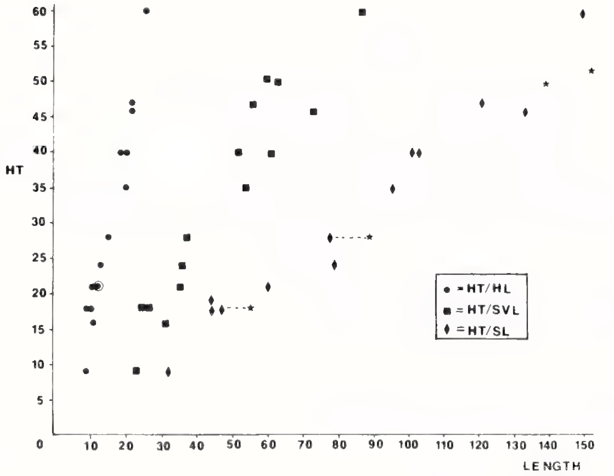

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Fig. 58.—*Allenypterus montanus,* graphs of height/head length (HT/HL), height/snout–vent length (HT/SVL), and height/standard length (HT/SL). Stars indicate total length measurements on specimens with terminal lobes.

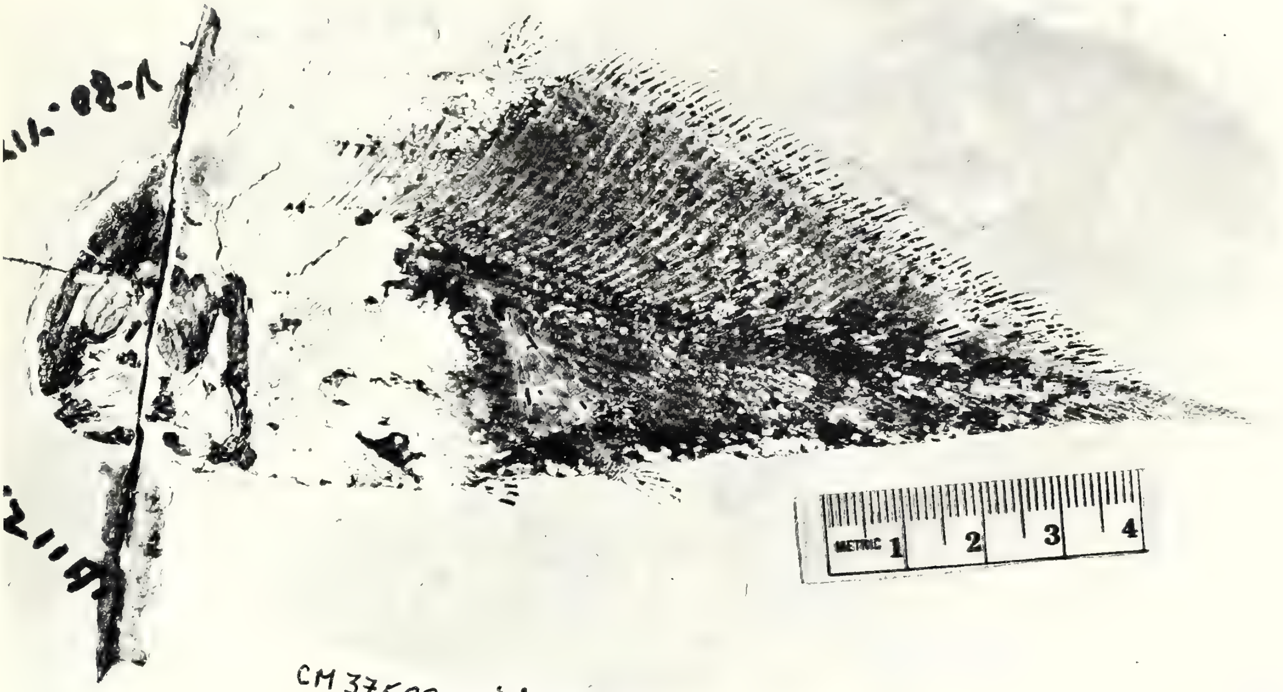


Fig. 59.—*Allenypterus montanus.* CM 37509a. Scale in mm.

There are indications from the three-dimensionally preserved head of MV 2555 that the lateral supraorbitals did indeed lay more on the lateral aspect of the living fish, while the more mesial bones faced dorsally. The two series of bones would then have been positioned almost at right angles to each other and to the lateral line canal. There may have been strong structural advantages to the fusion of the mesial supraorbital series with the parietal series.

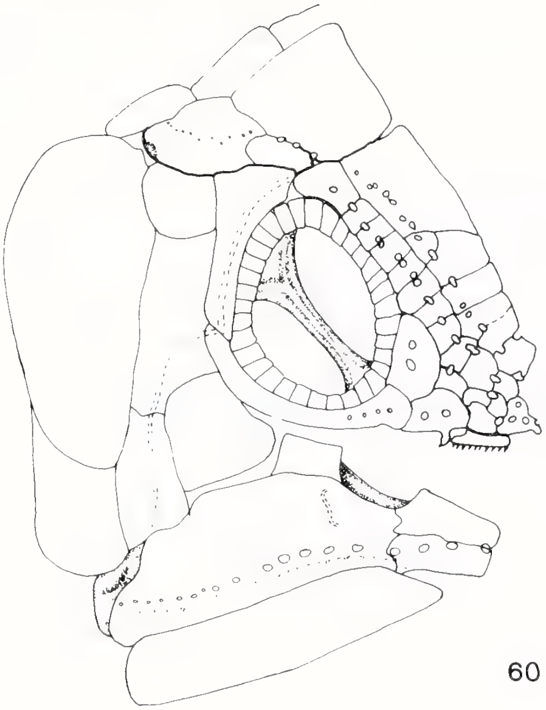
Filling of the supraorbital canal itself by calcite clearly shows, in CM 27286 and MV 5381, that there was a commissure between supraorbital canals at the level of the last postrostral, as is also suggested by the pattern of the pores in the surrounding bones (Figs. 60, 65). There also seems to be an ethmoid commissure through the lateral rostrals and rostral, and there are ample pores to suggest that there were parasagittal connecting commissures as well (Figs. 60, 65).

Three accessory elements lateral to the most anterior three lateral supraorbitals are emarginated both dorsally and ventrally for pores. Ventral to these elements and posterior to the rostral are a thin anterolateral and posterolateral rostral, each with very large pores. The posterolateral rostral also bears the descending nasal prong, against which the posterior end of the premaxilla abuts. The antorbital forms the anterior border of the orbit and bears two to three large pores, but it cannot be determined whether these pores are associated with the posterior pores of a rostral organ as in *Latimeria* (Millot and Anthony, 1958) or with an antorbital branch of the infraorbital lateral line canal (posterior lateral commissure, Fig. 74). All bones of the ethmosphenoid moiety are tightly abutted against one another.

Cheek.—The lacrimojugal and cheek bones are all thin, and lateral line canals and pores are difficult to trace. All bones are vertically oriented and, except for the postorbital, deeply overlapping (Fig. 60). The anterior margin of the postorbital is level with the intracranial joint. The preoperculum overlaps the posterior end of the lower jaw.

The operculum has a well developed articular facet that fits in a condyle near the posterolateral corner of the tabular. It cannot be determined whether this might represent the fusion of hyomandibular and opercular elements. The suboperculum is thin but prominent.

Oticooccipital.—The anterior end of the otic canal



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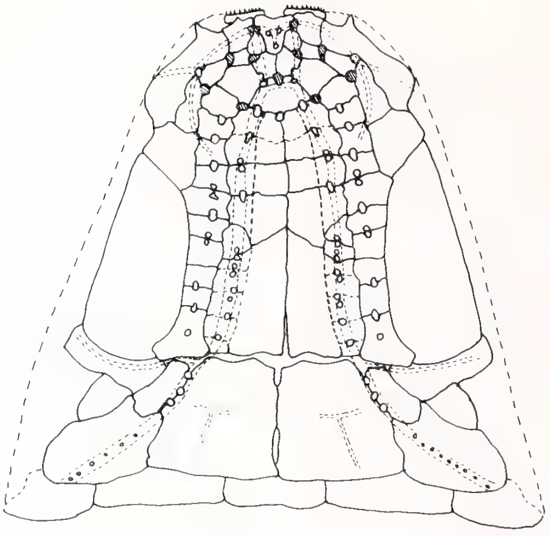

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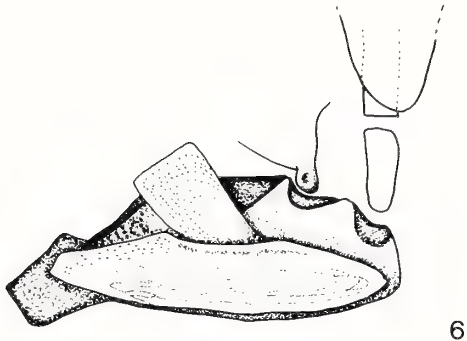

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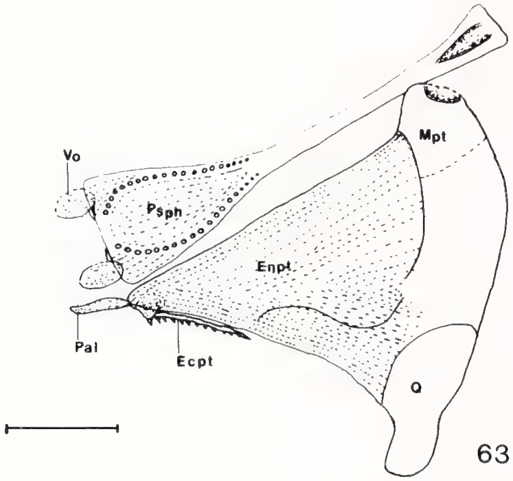

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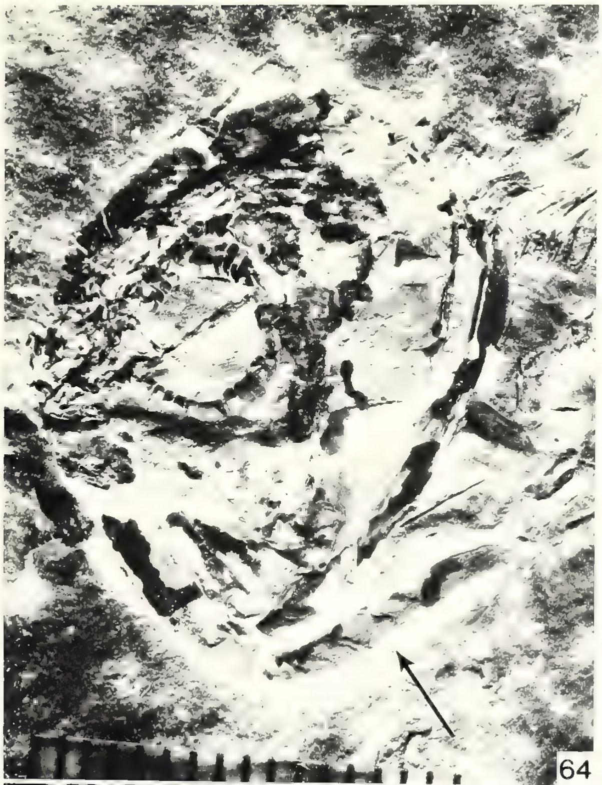
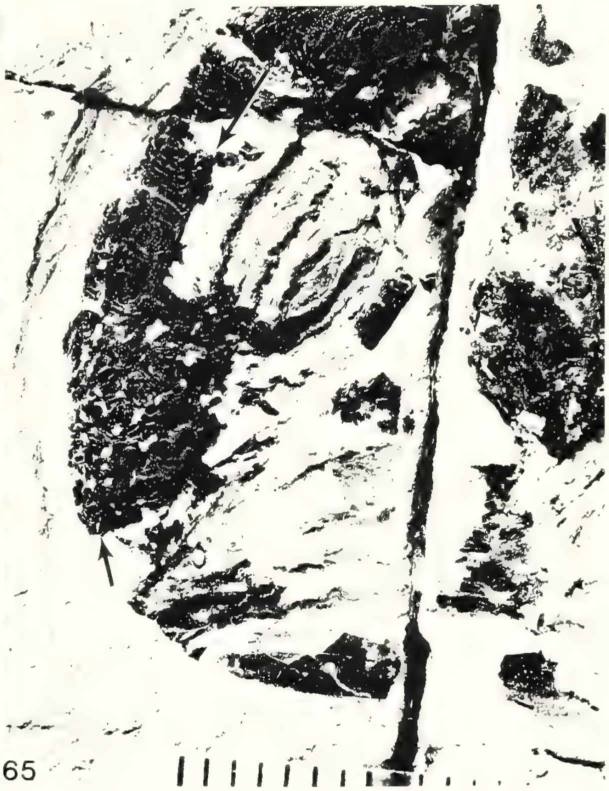
Fig. 60.—*Allenypterus montanus,* restoration of the bones of the lateral surface of the head, based on MV 3091, 5381.
Fig. 61.—*Allenypterus montanus,* restoration of the bones of the head in dorsal view, based on CM 27286, 27287, 37509.
Fig. 62.—*Allenypterus montanus,* internal view of lower jaw, based on MV 2949, CM 27287 and 37509.
Fig. 63.—*Allenypterus montanus,* palate and parasphenoid of CM 27286. See Fig. 64.

is beneath the supratemporal-postparietal suture, and gives off several large pores between the two bones (Figs. 61, 64). The tabular is greatly extended posterolaterally; much of the tabular, however, is unornamented. The posterior wall of the dorsal end of the spiracular canal is formed by the tabular with a contribution from the supratemporal. Pit lines in the postparietals are variable but often T-shaped, the posterior pit line extending to the rear margin of the postparietal. Contralateral postparietals are never sutured together in smaller individuals (Fig. 64) and rarely firmly joined even in the largest specimens.

There are 5 bones in the extrascapular series. Canals cannot be definitely traced in these bones. The posttemporal, if present, was small and thin.

Palate, lower jaws, and branchials.—The palate of *A. montanus* is relatively short and quite high in





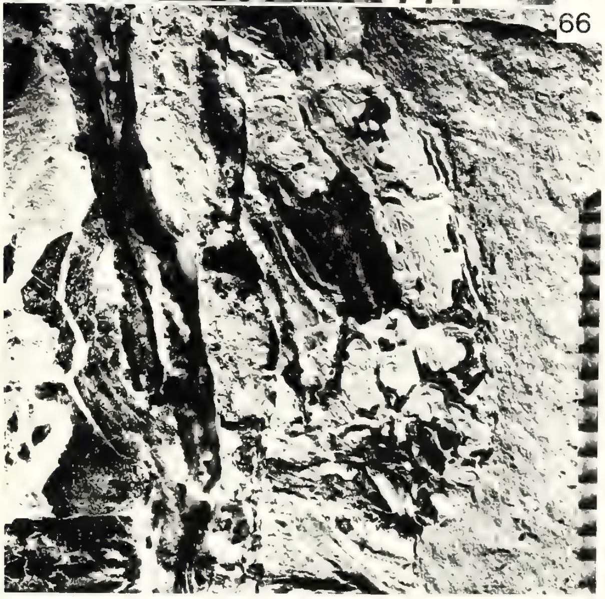


Fig. 64.—*Allenypterus montanus,* CM 27286, lateral view of head. Arrow points to median ventral scale shield. Scale in mm.
Fig. 65.—*Allenypterus montanus,* CM 37509a, anterior part of head. Arrows indicate dorsal midline. Scale in mm.
Fig. 66.—*Allenypterus montanus,* CM 37509b, anterior part of head. Scale in mm.

proportion to the head. The location of the external projection of the quadrate-articular joint at the level of the rear of the orbit in those specimens preserved with depressed heads is farther forward than in any other coelacanth except "*Diplurus*" *newarki* (Schaeffer, 1952). The palate bears relatively straight lines of fine denticulations divergent from the anterior end of the endopterygoid. The autopalatine is rarely seen and may have been weakly ossified; dermopalatines are thin and bear very fine teeth. The palate lacks any trace of a notch or facet for the reception of a basipterygoid process or basal articulation with the braincase.

The anterior end of the lower jaw, consisting of dentary occlusally and splenial below, describes an obtuse angle with the long axis of the angular. The dorsal edge of the angular shows a diastema, or concavity between the posterior end of the dentary and the coronoid. The mandibular canal exits through large pores in the splenial and anterior part of the angular, and continues rearward through finer pores, to pass from visibility at the posterior end of the angular. The pores of the canal do not curve upward posterior to the jaw articulation. The rear margin of the lateral surface of the lower jaw is separately ornamented and may represent coossification of a dermal element with the underlying retroarticular region of the articular (Fig. 60). In mesial view, fine teeth on one or more very thin plates line the dentary, and a thin precoronoid is continuous between the posterior end of the dentary and the prominent coronoid (Fig. 62). The posteroventral end of the coronoid lies mesial to the anterior end of the articular ossification, that in turn is apparently only coossified with the angular ventral and lateral to the articular facet. Several specimens, such as CM 27287, suggest that the retroarticular and articular regions of Meckel's cartilage ossify separately and fuse relatively late in development. The symplectic facet is located posterior and ventral to the articular facet. The prearticular spans the entire lower jaw from below the symplectic facet to the ventromesial bend in the dentary-splenial. The symplectic and epihyal are visible in MV 2949, the ventral end of the epihyal coinciding with the ventral edge of the operculum, the symplectic underlying the suboperculum.

The operculum bears an anterodorsal process extended from a slight ridge on its mesial surface that articulates with the posterolateral edge of the tabular. As this would coincide with the position and articulation of the hyomandibular with the braincase, we suggest that the hyomandibular has fused to the operculum.

The branchial arches do not appear to differ significantly from those of other coelacanths, apparently lacking pharyngobranchial elements. The arches all bear long, delicate gill rakers, however.

Shoulder girdle.—The anocleithrum has a slight but clear anterodorsal bend that renders it S-shaped in lateral view; it lacks evident contact with the head (Fig. 57). The cleithrum is quite elongate, with an ornament of long, thin vertical lines. The anteroventral process of the cleithrum and the posterodorsal, or cleithral process of the clavicle are thin and elongate, both overlapped by the extensive extracleithrum (Fig. 59). The clavicles are thickened and posteriorly expanded in the ventral midline, and do not suture across the midline. The thickened, deep and highly overlapping median ventral scale row, extending from the posterior ends of the clavicles to the middle of the pelvic plates, remains attached to these elements even after severe postmortem disruption of the abdominal cavity (Fig. 64). It must be presumed that there were strong ligamentous attachments among these elements.

Postcranial skeleton.—An ossified swim bladder is present.

The first six neural arches are wide, stout and closely fitted, with short neural spines only upon the last three. The remainder of the axial elements are as in other coelacanths (Fig. 57). The first dorsal fin plate is rounded, showing no trace of fusion from supraneural elements. The second dorsal fin plate is simple, rounded, and its shaft is intercalated between two neural spines, usually the 11th and 12th abdominal neurals. The epichordal lobe of the caudal fin begins one or two segments behind the end of the second dorsal fin, 8 segments in advance of the first caudal vertebral element.

The pelvic plates are large, high, very thin triangular elements intimately associated with the posterior end of the median ventral scale shield. They seem to lack significant perichondral ossification. The pelvic fins are placed at the rear of the abdominal cavity, immediately in advance of the anal fin, and the anus is located between the pelvic fins. There seems to be no visible possibility of extension of the gut behind the anus. Gut infillings have been found; these consist of amorphous calcium phosphate and never contain recognizable material on gross examination.

The anal fin plate is supported below the first haemal spine, against the anterior face of the second haemal, and is anteroposteriorly elongated. Separate infrahaemal elements begin at the sixth haemal spine; there may be up to 45 infrahaemals. The fin rays of the ventral caudal lobe are miniscule, not articulated, and occur in 2:1 ratio with their endoskeletal supports from about the 36th haemal spine. They grade into an even finer series of rays posterior to the end of the caudal endoskeleton, on the vermiform extension of the body axis (Fig. 59).

The last three trunk segments and the first sixteen caudal segments of MV 5381 seem to show very thin, faint ossification of the vertebral centra consisting of fused dorsal and ventral elements. Details, however, cannot be resolved and cannot be confirmed on any other specimen.

Discussion.—The unique body form of *Allenypterus montanus* and the ecomorphological relationships of the remainder of the Bear Gulch coelacanths have been discussed elsewhere (Lund et al., in press) and need not be elaborated upon here. In summary, however, *A. montanus* is well adapted to a shelter dwelling life and extremely slow undulatory motion through the use of the long low epichordal caudal fin. High maneuverability is inherent in the use of the high, compressed body with the size and distribution of the paired and median fins around the center of buoyancy in the short trunk. The total lack of surface area at the caudal extremity, an aspect ratio effectively of zero, indicates that rapid acceleration for escape from predation could be provided only by a quick stroke of the caudal region of the body and would be of low effectiveness. *Allenypterus* would be very unlikely to survive outside the shelter of algal or sponge thickets. The small ventroterminal mouth, restricted gape, tiny teeth and long gill rakers indicate a feeder upon rather small and relatively soft bodied organisms.

The uniquely adapted body form of *A. montanus* does not, at this time, constitute sufficient reason to place it in its own, and necessarily monotypic, family. It shares an equal number of unique and probably derived characters with *Hadronector* and *Polyosteorhynchus.* It also shares the high ratio of fin rays to endoskeletal supports with *Lochmocercus, Diplocercides,* and *Coelacanthopsis curta*: a primitive character of little systematic or phylogenetic utility.

Suborder *Incertae sedis*

Genus ***Lochmocercus*** Lund and Lund, 1984

Type species.—*Lochmocercus aciculodontus* Lund and Lund, 1984.

Provisional diagnosis.—Coelacanths with relatively long trunks. Moderate size supratemporal bone bears pores for anterior end of otic canal; antorbital with two pores, lacrimojugal with pores, and complete cheek tightly fit together. Anterior margin of postorbital close to intracranial joint. Lower jaw lacks anterior angular diastema and margin continuous from dentary through precoronoid to anterior margin of coronoid. Dentary and precoronoid bear a row of large teeth. Opercular flap with both operculum and suboperculum. Anocleithrum stout and may have contacted rear of skull, cleithrum short with a long anteroventral process, clavicles short and extracleithrum tightly sutured to cleithrum. First dorsal fin plate shows ventral digitiform processes, second dorsal plate simple, rounded above and articulates dorsally with presumed fin axis. Pelvic plate quadrangular and lacking in significant perichondral bone: its axial elements are ossified. Fin rays of caudal fin in 2:1 ratio to endoskeletal supports.

Discussion.—The genus *Lochmocercus* resembles members of the Hadronectoroidei in characters of bones of the cheek, oticooccipital moiety, lower jaw, and the supports for the dorsal and pelvic fins, and in doing so is conspicuously divergent from *Diplocercides.* There is insufficient information on critical characters in the ethmosphenoid moiety, due to a lack of well preserved specimens, to definitively assign this genus to either suprageneric group. One other coelacanth taxon besides *Diplocercides* and *Allenypterus* has a 2:1 ratio of caudal fin rays to endoskeletal supports, *Coelacanthopsis curta* Traquair (1905). The type and only specimen of *C. curta* has had the midsection of the body faulted under the caudal region, and has no distinguishable cranial elements, so comparisons are difficult. The shoulder girdle of *C. curta,* however, is indistinguishable in proportions or ornamentaation from that of *Lochmocercus.* It is felt that future speciens of *C. curta,* were they to be found, would indeed be recognizable and that the name cannot be buried or obliterated.

Lochmocercus aciculodontus Lund and Lund, 1984
Figs. 67–70

Previous reference.—"Bushy tail," Lund et al., in press, Fig. 1.—*Lochmocercus aciculodontus* Lund and Lund, 1984.

Type specimen.—MV 6218.

Referred specimens.—CM 27406, 30715, 35201.

Horizon and locality.—Namurian A (E2B), Lower Carboniferous Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Provisional diagnosis.—Trunk long relative to height, size to over 92 mm standard length. Bones of skull roof sparsely ornamented with coarse tubercles, other external head bones more densely ornamented. There are 31–33 neural spines in trunk, 4+23–28 fin rays in both dorsal and ventral aspects

Table 5.—*Proportional statistics of* Lochmocercus aciculodontus. *Abbreviations as in Table 1.*

Statistics	Max. ht./SL	HL/SL	GL/HL	GL/SL	GL/LJL	Asp. R.
N	1	3	2	2	2	1
Mean	.4487	.2427	.444	.1048	.5336	.9524
SD	—	.0219	.0058	.013	.005	
Var.	—	.0003	.00001	.00008	.00001	

of caudal fin, rays of first dorsal fin are 3+8, of second dorsal fin are 2+9. Caudal outline is elliptical. Proportional characters given in Table 5.

Description.—*L. aciculodontus* is the rarest and the most poorly preserved of the Bear Gulch coelacanths. The rostral region is not completely preserved on any single specimen, nor is there any complete axial skeleton attached to a head. The parasphenoid of the holotype, MV 6044, can be seen posteroventral to the anal fin in Fig. 67. Thus there are few reliable details of the ethmosphenoid moiety available at present. Further, there is no convincing evidence that the largest available specimen represents a mature individual. Nevertheless, many salient details of the osteology are available.

The only available ethmosphenoid moiety of the skull roof has been disrupted (Figs. 67, 68). Large parietals, lacking any trace of a lateral line canal form the supraorbital region, and there are indications of at least two pairs of frontonasals anteriorly. Laterally, a single series of supraorbital bones is visible, approximately six of which roofed the orbital rim. The antorbital is large, and bears two pores as if for the rostral organ, and anteriorly the posterolateral rostral bears few, large pores for the infraorbital lateral line canal and an anteroventral nasal prong. A dislocated element immediately anterior to the posterolateral rostral is probably an anterolateral rostral; it is perforated or bordered by at least one pore. The premaxilla is seen as a low strip of bone bearing a few long, sharp teeth.

The lacrimojugal is unusual in showing a long series of prominent, although small, infraorbital canal pores. The infraorbital canal passes from the middorsal margin of the heavy postorbital to the skull roof at the anterior end of the supratemporal. The prespiracular is large, thin and rounded, forming the spiracular operculum. The jugal lateral line canal turns ventrad to enter the anterior margin of the preoperculum. A quadratojugal pit line cannot be resolved.

The opercular series contains a long, ventrally tapering operculum and a tall, narrow suboperculum.

The dermal bones of the oticooccipital moiety of the skull consist of large postparietals bordered posterolaterally by the supratemporals and tabulars. The supratemporal does not extend forward to the in-

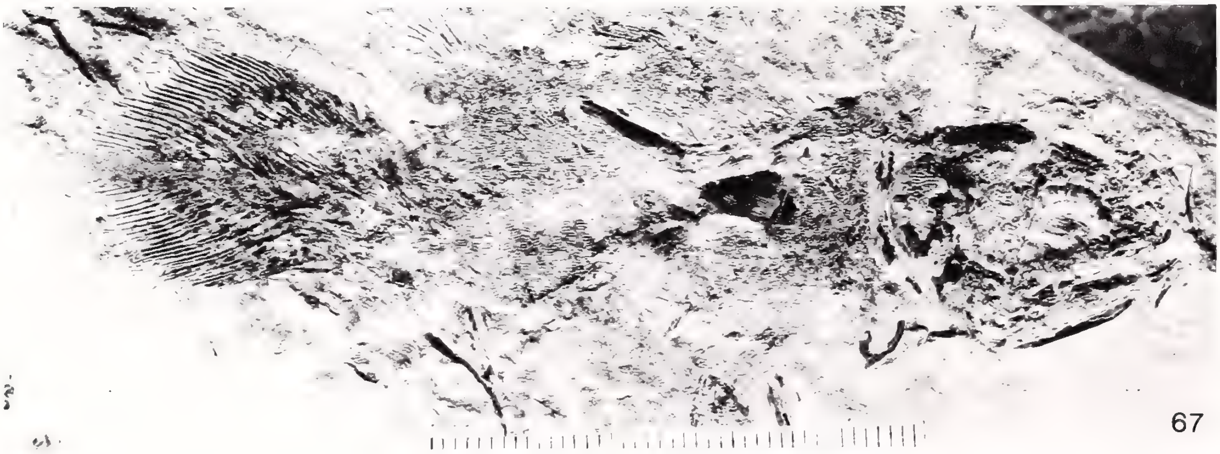


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Fig. 67.—*Lochmocercus aciculodontus,* type, MV 6044. Scale in mm.

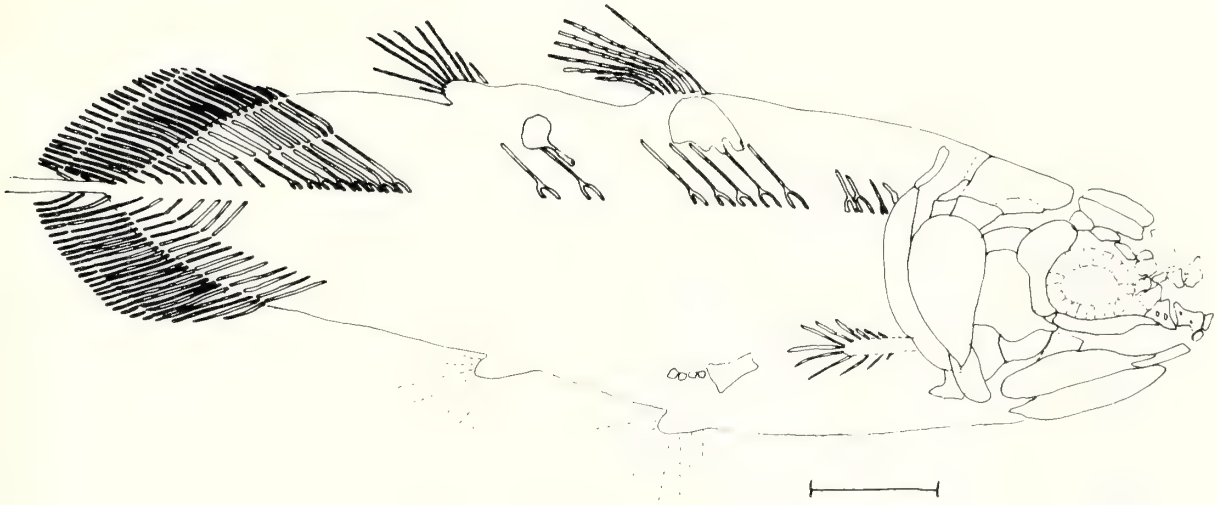


Fig. 68.—*Lochmocercus aciculodontus,* restoration based on MV 6044.

tracranial joint. A branch of the supraorbital lateral line canal enters the anterolateral margin of the postparietal anterior to the supratemporal and ends in a large pore at the level of the middle of the supratemporal. The transverse supraorbital commissure apparently joins the infraorbital canal to form the otic canal, which appears to continue through the supratemporal into the tabular. Several large pores are visible in the tabular. Ornamentation is sparse on the oticooccipital moiety.

There are five very thin bones in the transverse occipital commissure.

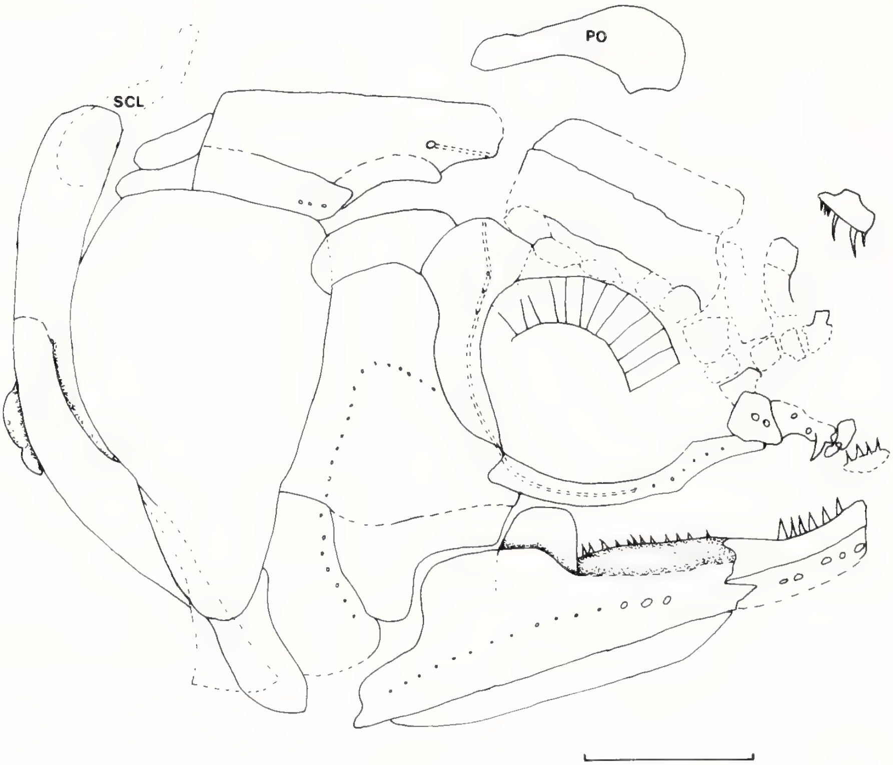
The autopalatine ossification is stout and triangular, articulating with the ethmoid region lateral to large, heavily toothed prevomers (Fig. 70). The ectopterygoid extends to the level of the coronoid on the lower jaw. The endopterygoid bears few, relatively coarse ridges paralleling its dorsal margin. The metapterygoid is stout, and articulates with the relatively short antotic process. The quadrate projects significantly posterior to the level of the antotic process. There is no visible indication on the palate of articulation with any process of the braincase.

The oral margin of the dentary bears large, long sharp teeth, and is continuous posteriorly with the dorsal edge of a precoronoid that also bears a row of teeth (Fig. 70). The oral margin of these two bones extends uniformly posteriad to the base of the coronoid. While there is no angular diastema, the oral margin of the dentary and the precoronoid are mesially inset in relation to the lateral laminae of the dentary and the angular. The splenial bears a few large pores anteriorly, with relatively small pores of the mandibular lateral line continuing through the angular. The articular element is as strongly ossified along its anterior surface as along the posteroventral surface of its quadrate condylar fossa. The retroarticular area of Meckel's cartilage seems to be separately ossified (Fig. 70).

Branchial arches are not well known.

The shoulder girdle is most noteworthy for being a very tightly integrated structure, lacking the relatively loose and flexible association of clavicle, extracleithrum and cleithrum seen in most other coelacanths. There does seem to be an extracleithrum, and a large one, but it is tightly held to the associated bones and lines of ornamentation are continuous across the cleithrum-extracleithrum boundary. There is ossification in the scapulocoracoid cartilage, but details cannot be resolved.

Discussion.—There is scarcely adequate information about the osteology of *L. aciculodontus* upon which to judge its relationships. There are several noteworthy primitive characters, such as the relationships of the bones of the lower jaw, that differentiate it most strongly from *Hadronector* and *Allenypterus*; the caudal fin ray ratio, that differentiates it from *Hadronector* and *Polyosteorhynchus*; and the stout anocleithrum, tight association of cleithrum and clavicle, and the passage of the supraorbital canal into the postparietal, that separate it from all Hadronectoroidei. The apparent single supraorbital



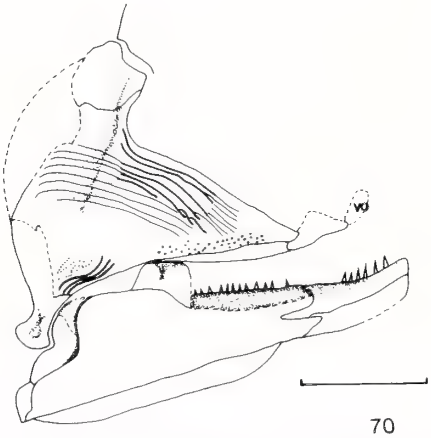


Fig. 69.—*Lochmocercus aciculodontus*, reconstruction of the head of MV 6044.
Fig. 70.—*Lochmocercus aciculodontus*, palate and lower jaw of MV 6044.

series contrasts strongly with the complexities of *Polyosteorhynchus, Allenypterus* and *Hadronector*. The supratemporal is reduced by comparison with the three Hadronectoroidei, but large in comparison with Coelacanthoidei. Ornamentation of the skull roof is sparse, but this could signify nothing more than rather immature individuals.

Lochmocercus shares a suite of primitive characters with Hadronectoroidei but with no member of the Coelacanthoidei. These include the five bones in the tightly knit cheek, the supratemporal, the suboperculum, and the apparent lack of a basipterygoid process. It shares with *Allenypterus* as well as the coelacanthoid *Diplocercides* only one common character, the primitively high caudal fin ray : endoskeletal support ratio.

DISCUSSION

GROWTH, DEVELOPMENT, AND SPECIES IDENTIFICATION

Several characteristics have, in the past, been suggested or used in attempts to identify and diagnose species of coelacanths (Schaeffer, 1952; Moy-Thomas, 1937; Forey, 1981). Scale ornamentation, for instance has been used to diagnose the "genus" *Chagrinia* (Schaeffer, 1962), and to place various fish into the "species" *Rhabdoderma elegans* without cranial osteological knowledge. Virtually nothing has been said about scale ornamentation in the descriptive portion of this paper, for several reasons. The first is simply that scales of *Caridosuctor* have an ornament of few, tightly packed lines slightly convergent at the posterior midline of the scale, but that the variation accounted for by position on the body and by specimen size prevents further analysis. Scales are not present on the 30 mm *Caridosuctor* and unornamented on the 42 mm specimen. Growth characteristics of the other species are more complex. Scales of *Hadronector, Allenypterus,* and *Polyosteorhynchus* specimens, when large, are all similarly ornamented with few, straight, relatively thick lines and are indistinguishable. The scales of *Lochmocercus* are tuberculated in the one specimen with scales. However, *Allenypterus* up to the 44 mm specimen are faint and indistinguishable, and specimens of larger sizes rarely preserve with distinct scales, until over 100 mm in length. It is not known at what length *Polyosteorhynchus* develops scales, as neither of the very well preserved 35 mm specimens has scales and the poorly preserved intermediate sized specimen does not show scales. The condition for small *Hadronector* is unknown. Although there are two small specimens of *Lochmocercus,* both lacking scales, this may have been a preservational factor. It has proved futile to use scales for identification within the Bear Gulch coelacanths.

Ornamentation, particularly of the gular or opercular, has been traditionally used to erect species in the British Carboniferous. This matter has been explored in regard to the *R. elegans-R. lepturus* question, above, but should be amplified upon. All species of coelacanths in the Bear Gulch are born without external ornamentation of any kind. Generally, only the fin rays, axial skeleton, shoulder girdle, lower jaws, and branchial arches are evident in the smallest specimens of all species. Among the members of the Hadronectoroidei, in *Allenypterus* and *Polyosteorhynchus* the smallest individuals are between 28 and 35 mm long, but individuals at around 70–80 mm display the first signs of virtually identical ornamentation (Fig. 52). The ornamentation of the 92 mm *Lochmocercus aciculodontus* is coarse and sparse, characteristic of *Allenypterus* and at about the same size. Specimens of *P. simplex* over 100 mm have an opercular and cheek ornamentation clearly distinguishable from that of any other coelacanth in the Bear Gulch (Figs. 49, 51), but variation in the osteology of the cheek is significant. Large *Hadronector* may be distinguishable from other coelacanths in the Bear Gulch fauna on the basis of the combined ornamentation and bone thickness, simply because no other has thick cheek bones. Finally, ornamentation of *Caridosuctor* on the gulars and operculum is usually recognizable, but these elements are primarily recognizable on the basis of size and proportions, the articulation with the tabular, and full knowledge of the tremendous variability in ornamental pattern. Even the bones of the cheek of *C. populosum* may be ornamented or unornamented at any given size up to that of the largest individuals. The use of ornamentation, without correlating it with size and proportions over a large range of sizes, is what led Newberry (1856) to name three species of *Rhabdoderma* from Linton, Ohio, only to later question his own taxa (Newberry, 1873). The use of ornamentation to diagnose species, at the level of detail discrimination that characterizes paleontologic practice, is an exercise in futility.

Vertebral counts have proved useful in the Bear Gulch coelacanths only with great caution. The ability to discriminate regions of the column makes it possible to avoid the uncertainties of covered anterior neurals. Counts of caudal segments are highly uncertain in light of the progressive ossification of the most posterior neural and haemal spines. Suites of specimens within a fauna can be distinguished with the help of vertebral counts, but not solely by use of this character.

Growth characteristics and proportions of the Bear Gulch coelacanths are all extremely similar in pattern and diverge from a common set of body proportions in simple linear fashion separated by very fine, highly significant statistical differences (Table 6, Figs. 71, 72). Corresponding details of osteology show similar proportional differences. Among the most significant are those that can be related to functional separation of the species, such as gape length and aspect ratio (Table 6; Lund et al., in press), and the shape of the caudal fin. In this regard, however, it should be noted that the shape of the caudal fin

Table 6.—*Relationships among Bear Gulch coelacanth species and body ratiois.*

Statistics	Large				Small
	A.m.	*H.d.*	*P.s.*	*C.p.*	
$\frac{\text{Mx. ht.}}{\text{SL}}$	.3598	.3508	.3314	.2256	
	P.S.	*H.d.*	*A.m.*	*C.p.*	
$\frac{\text{HL}}{\text{SL}}$	.2288	.2062	.1874	.1596	
	C.p.	*H.d.*	*L.a.*	*P.S.*	*A.m.*
$\frac{\text{GL}}{\text{HL}}$	.4833	.4708	.444	.3895	.3598
	L.a.	*H.d.*	*P.S.*	*C.p.*	*A.m.*
$\frac{\text{GL}}{\text{SL}}$	.1048	.0957	.0934	.0796	.0666
	L.a.	*H.d.*	*P.S.*	*C.p.*	*A.m.*
$\frac{\text{GL}}{\text{LJL}}$	.5336	.5187	.5067	.4891	.4567
	H.d.	*P.S.*	*C.p.*	*A.m.*	
$\frac{\text{LJL}}{\text{SL}}$	.1869	.1801	.1584	.1434	
	H.d.	*P.S.*	*L.a.*	*C.p.*	*A.m.*
Asp. R.	1.188	1.133	.9524	.7989	

of *Polyosteorhynchus* changes from elliptical to square cut over its recorded size range. There are insufficient data to determine whether this is a gradual change or one that occurs in the transition from larval to adult conditions, as has been documented for many Bear Gulch actinopterygians (Lowney, 1980). It is also worth noting that while high growth rates of height parameters around the oticoccipital moiety of the head and the trunk of *Allenypterus* relative to long measures account for the greatest part of its unusual adult shape (Fig. 58), ratios of longitudinal parameters fit with the same degree of fine spacing as seen in the other coelacanths of the fauna (Figs. 71, 72, Table 6). These differences apply within the Bear Gulch fauna, but their utility in distinguishing species among faunas would appear to be very limited, given the possibility of character displacements with different interspecific interactions than the ones found herein.

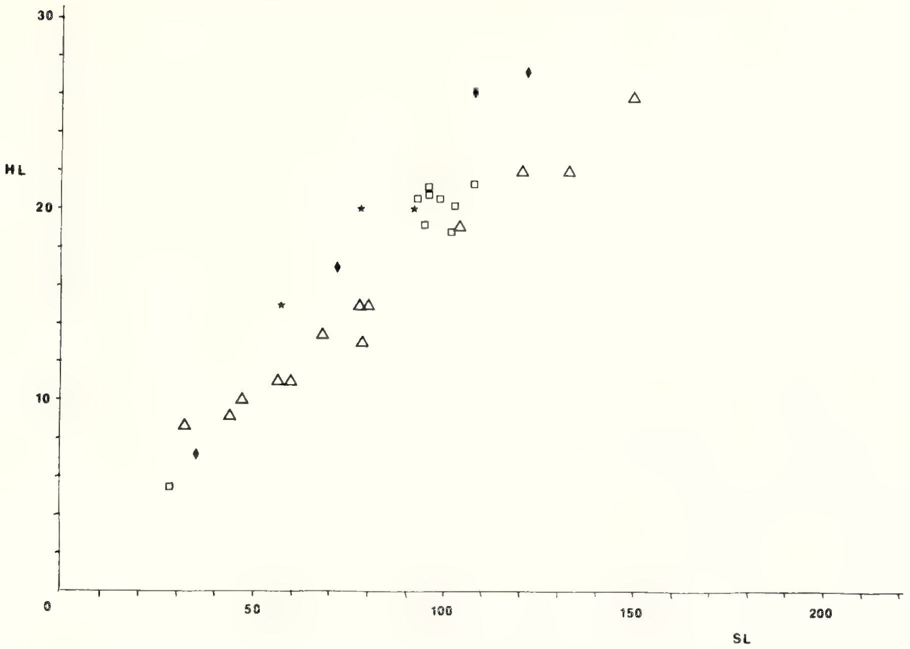
Attempts were made to analyze distance from the snout to the origins of dorsal fins one and two as in Schaeffer (1952), but it was found that intraspecific variation rendered this character meaningless in the Bear Gulch fauna and extremely suspect in the original application. There is no indication in specimens of *Rhabdoderma elegans* or of any Bear Gulch coelacanth of the extraordinarily long median lobe of the caudal fin that Schultze (1972) found in *R. exiguum* fetuses. There is a decrease in the median lobe : standard length ratio of *Caridosuctor* from .0785 at 79 mm to .0684 (N = 6) in the 120–140 mm range, to .0648 (N = 3) at the 179–182 mm range, to .0540 in the 200–220 mm range (N = 2). A similar decrease can be seen in *P. simplex.*

Nothing can be said about the growth of *Hadronector donbairdi* because specimens have only been reliably identified between 91–108 mm in standard length. This may be an artifact of sampling in view of the relative scarcity of the species, although assorted sizes are known for all other coelacanths. Of the remaining coelacanths, there is a striking disparity between the standard lengths of the two smallest, *C. populosum* 30 and 42 mm, and the majority of the specimens, starting at 79 mm (Fig. 72). The smallest *Caridosuctor* are considerably smaller than *Rhabdoderma,* which clearly had large yolked eggs. Among other known Rhabdodermatidae, the size range of yolk sac bearing individuals of *Rhabdoderma exiguum* is around 49–55 mm (Schultze, 1972, 1979), and the minimum known size of *R. elegans* is around 49 mm.

The reproductive mode of *Latimeria* involves probable internal fertilization (Griffith and Thomson, 1973), large yolked eggs, and fetuses that are retained in the oviduct of the mother without further maternal nutritional contribution and without a hard protective shell (Smith et al., 1975). The size of the unprotected eggs and fetuses of *Latimeria* virtually demands a strategy of perinatal care, as must the fetuses of *Rhabdoderma* and possibly *Caridosuctor.* Migration to a protected spawning ground could constitute such strategy.

There are morphological features found in the coelacanths with known relatively larger eggs that may be at least in part associated with prolonged retention of fetuses to larger absolute size at birth. These include the broad, medially articulated pelvic girdles, the shift to midabdominal location of the pelvics (see *Allenypterus* for the opposing condition), and the posterior extension of the peritoneal cavity. It must be pointed out that these features are shared by *Hadronector* and the Coelacanthoidei.

Retention of the fetus to an advanced size and migratory spawning are not correlated adaptations, but both constitute significant adaptations for perinatal care among vertebrates (Lund, 1980; Wourms, 1977). It is suggested that advanced retention of young represented the most significant adaptive advance of the Coelacanthoidei. The varying reproductive strategies of the "guild" of coelacanths in



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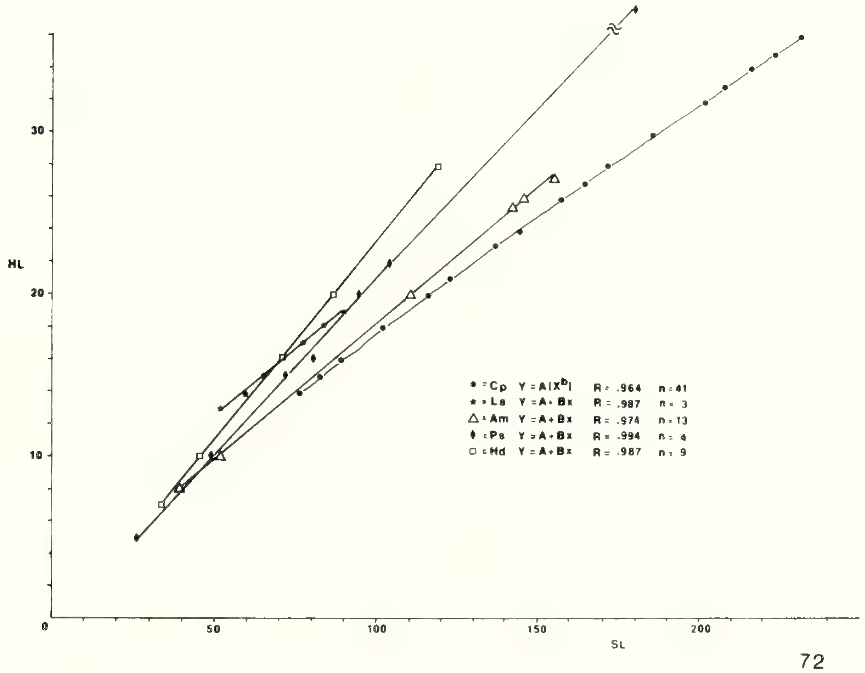

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Fig. 71.—Graphs of head length to standard length for *Allenypterus montanus* (triangles); *Hadronector donbairdi* (squares); *Lochmocercus aciculodontus* (stars); and *Polyosteorhynchus simplex* (diamonds).

Fig. 72.—Graph of regressions of head length to standard length for *Caridosuctor populosum* (Cp), *Lochmocercus aciculodontus* (La), *Allenypterus montanus* (Am), *Polyosteorhynchus simplex* (Ps), and *Hadronector donbairdi* (Hd).

the Bear Gulch fauna, however, are also significant. The coexistence of five species of coelacanths in the same, rather small basin could in part have been aided by resource partitioning based upon fine differences in feeding and swimming mechanisms (Table 6; Lund et al., in press; Schoener, 1974; Gatz, 1979). There is, however, very little overlap in potential resource utilization between groups of young fish differing as radically in size at first appearance as *Caridosuctor, Hadronector,* and the remainder of the Bear Gulch coelacanths.

Lateral Line Homologies

The lateral line canals, or more properly the neuromast organs, are vital landmarks in the determination of bone homologies among Placodermi (Ørvig, 1975; Miles, 1977) and Osteichthyes (Jarvik, 1948; Jollie, 1980; Westoll, 1949; Denison, 1968; Lowney, in press), and have a critical, if unclear, relationship to the process of induction of the dermal skeleton through the formation of sensory placodes from neural crest ectomesenchyme. The inductive process, while it need not be the concern of this article, is currently thought to work in a manner similar to that now known in the induction of ameloblast and dental papilla during odontogenesis (Kollar, 1978). Even in the Chondrichthyes and Acanthodii, where the formation of the dermal bones of the head is either absent or apparently unrelated to the lateral line canals, scales immediately adjoining the canals are modified in some manner (Miles, 1973; Zidek, 1976; Patterson, 1965), indicating that there is some inductive relationship. That this relationship is not a simple one is clear from studies of ontogenetic variation in many fish (Jarvik, 1948; Parrington, 1949; Jollie, 1980; Pehrson, 1947, for examples) including *H. donbairdi* and *A. montanus.*

The lateral line sensory canals of the heads of the gnathostome fishes display a series of variations upon a conservative pattern, many elements of which can be readily homologizable among the classes. The pattern consists of a limited number of longitudinal canals variably joined by segmentally arranged transverse canals (Ørvig, 1975; Jarvik, 1948; Stensiö, 1947; Westoll, 1949; Pehrson, 1947; Jollie, 1980; Lowney, in press). This pattern in turn corresponds sufficiently with the canal pattern seen in the carapace of various heterostracans (Säve-Söderbergh, 1941; Ørvig, 1975; Lowney, in press) that it can be accepted as a model for the primitive condition of the sensory canal system of the gnathostomes.

Complicating the study of the lateral line canal system and related bones among the Osteichthyes is that paleontological evidence has been so incomplete that little useful information could be added toward determination of the applicability of details of the model to evolutionary patterns within the class. The coelacanths have not previously provided sufficient information to document certain gross homologies, whereas the previously available actinopterygian evidence, particularly from the Paleozoic, has been very limited (Stensiö, 1947). Lateral line canal information from the Bear Gulch Osteichthyes has added considerable information.

In spite of considerable variation among taxonomic groups, the homologies and the basic names of the longitudinal canals and several of the transverse canals seem to be agreed upon (Fig. 73). Thus the longitudinal canals are the supraorbital, the otic (epibranchial), infraorbital (including jugal, perhaps including supramaxillary) and the mandibular. These canals are variously joined by cross commissures. The rostral region is very rarely preserved and yields the least comparative information but may have two commissures across the dorsal midline, the ethmoid anteriorly and the antorbital behind it. Two lateral commissures are indicated between the supraorbital and infraorbital canals antorbitally, the anterior lateral and posterior lateral commissures. Posteriorly, the supraorbital and otic canals may be joined by at least two major lateral commissures, the transverse supraorbital and the transverse otic. An anterodorsal branch of the postorbital, the supraorbital branch of Miles (1977) has been suggested as a branch of a separate longitudinal epibranchial canal by Poplin (1973) and supported by Thomson and Campbell (1971). Evidence for this branch can also be found in part in heterostracans (Ørvig, 1975) and Actinopterygii (Lowney, in press) and suggests that it may be involved in links between the supraorbital and otic canals (Poplin, 1973). The otic canals are joined across the dorsal midline by the occipital (supratemporal) commissure, at or behind the rear margin of the braincase. The infraorbital canal may continue posterior to the orbit as the jugal canal, although the homologies here are far from agreed upon. It is connected to the otic canal dorsally by the postorbital canal and ends at the preopercular canal, which spans the side of the head from otic to mandibular canals. Additionally, there are reports of an opercular transverse canal (Lowney, 1980). Phylogenetic regression of lateral line canals may leave visible indicators in bones in the form of pit lines, or simply clusters or rows of naked neuro-

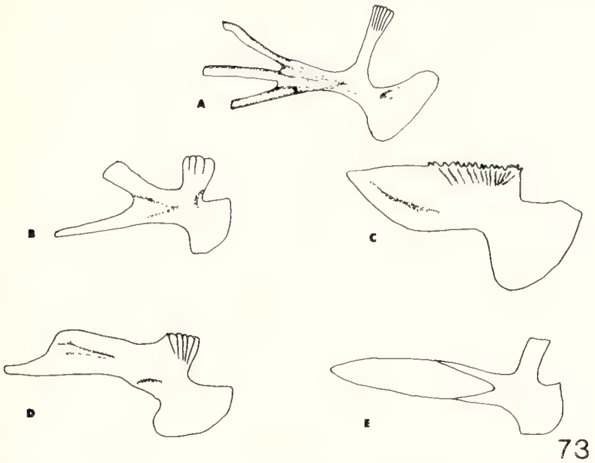

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Fig. 73.—Pelvic plates of certain coelacanths. A) *Rhabdoderma elegans,* CM 23018; B) *Diplurus newarki* (after Schaeffer, 1952); C) *Wimania sinuosa* (after Stensiö, 1921); D) *Coelacanthus granulatus* (after Moy-Thomas and Westoll, 1935); E) *Undina* cf. *U. minuta* (after Schaeffer, 1941).

masts without traces upon the underlying bone (Freihofer, 1978; Stensiö, 1947); these sensory organs usually retain their normal innervations and relationships to the remainder of the lateral line system.

In some coelacanths of the Bear Gulch limestone, the supraorbital canal extends from a clear antorbital commissure to an intersection with the postorbital part of the infraorbital canal, receiving an apparent posterior transverse commissure anterior to the orbit. An ethmoid, anterior transverse and antorbital commissure can be demonstrated in *Allenypterus* (Fig. 61) and are strongly suggested for *Hadronector* and *Polyosteorhynchus* (Figs. 44, 55). Shortening of the snout seems to have been linked to the elimination of the antorbital commissure and posterior lateral commissure in Coelacanthoidei (*Caridosuctor,* Fig. 75C). Details of the intersection of supraorbital and postorbital canals are usually obscured by the intracranial joint, but in *Lochmocercus* the supraorbital canal continues into the postparietal to end at a pit and posterior pit line (Fig. 69). The junction of supraorbital and postorbital canals in this genus is clearly associated with another canal branch, possibly the transverse supraorbital commissure. Among other coelacanths, the postparietal contains an isolated series of pit lines, the anterior and posterior in *Polyosteorhynchus,* possibly a continuous pit line in *R. lepturus,* and posterior and transverse pit lines in *Hadronector* and *Allenypterus.*

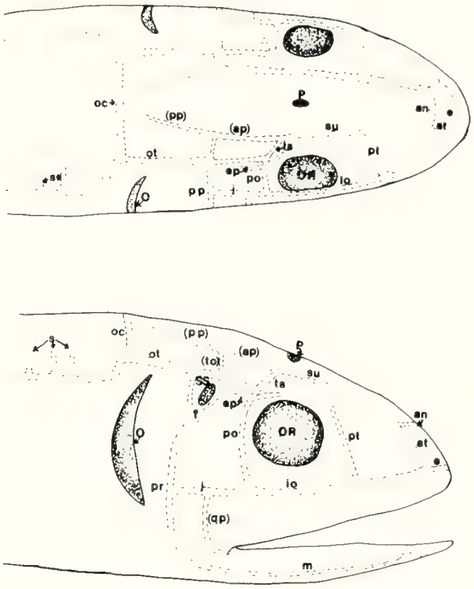

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Fig. 74.—Idealized lateral line canal and pit line patterns of Osteichthyes. Abbreviations (sensory canals usually expressed as pit lines are in parentheses): (ap) anterior pit line; an, antorbital commissure; at, anterior transverse commissure; e, ethmoid commissure; ep, epibranchial branch; i, infraorbital canal; j, jugal (supramaxillary) canal; m, mandibular canal; O, opercular slit; oc, occipital (supratemporal) commissure; OR, orbit; Ot, otic canal; P, pineal (parietal) foramen; (PP) posterior pit line; pt, posterior transverse commissure; po, postorbital canal; pr, preopercular canal; (qp) quadratojugal pit line (oral canal); s, segmental trunk canals; ss, spiracular slit; su, supraorbital canal; (to) transverse otic commissure (transverse pit line) ts, transverse supraorbital commissure.

In *Porolepis* and *Holoptychius* the supraorbital canal receives the postorbital canal directly, and continues posteriorly to end at the transverse and posterior pit lines (Fig. 76A, D). A transverse canal at the position of the transverse otic commissure carries the lateral line into the tabular and in essence to an extremely short otic canal. The canal pattern in the narrow roofed *Osteolepis* and *Eusthenopteron* is essentially as in later or more specialized coelacanths (Fig. 76B, E). Most Devonian dipnoans show a prominent anterior medial bend in the supraorbital canals, as do crossopterygians. Only *Chirodipterus* and *Dipterus valenciennesi* are indicated to have an antorbital commissure (Miles, 1977) at this point. Some Devonian dipnoans show complete or apparent connections through what may be a transverse supraorbital commissure with the supraorbital canal, such as *Dipterus valenciennesi* (Westoll, 1949; Fig. 76C), *Uranolophus* (Denison, 1968), and *Stomiahykus* (Bernacsek, 1977), whereas in *Dipno-*

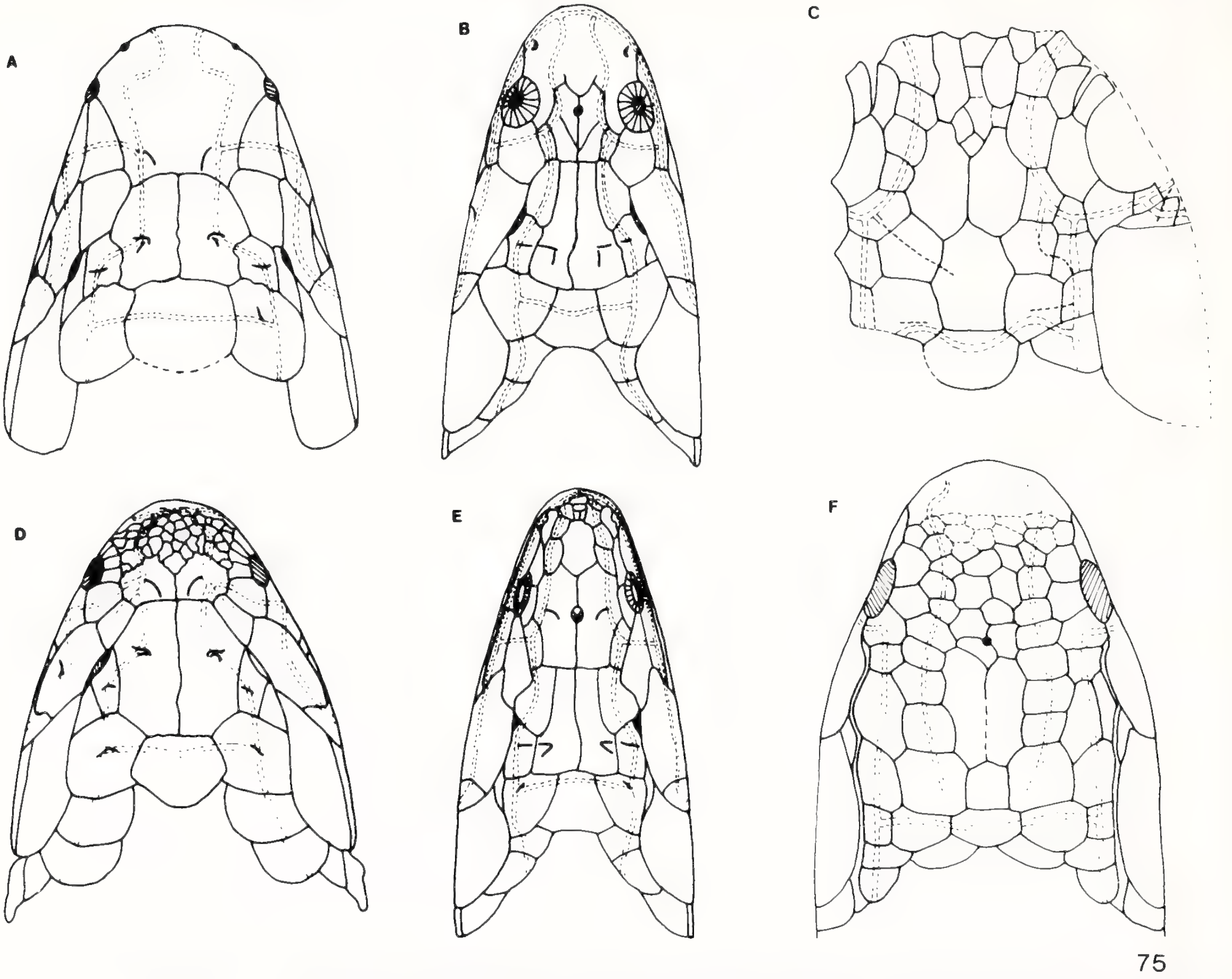

Fig. 75.—Coelacanth skulls. A) *Euporosteus eifeliensis,* ethnosphenoid (after Stensiö, 1937); B) *Allenypterus montanus*; C) *Caridosuctor populosum*; D) *Diplocercides kayseri* (after Stensiö, 1937); E) *Diplurus newarki* (after Schaeffer, 1952); F) *Macropoma mantelli* (after Watson, 1921).

rhynchus sussmilchi the supraorbital canal extends to the skull rear with no evident connection to the otic canal (Westoll, 1949, Fig. 76F). Many lungfish show regression of the supraorbital canal to pit lines posterior to the commissure, producing a pattern very similar to that of the later coelacanths, crossopterygians and many actinopterygians.

At the rostral region the apparent supraorbital canal meets the infraorbital canal anteriorly and crosses the midline at the ethmoid commissure in porolepids, osteolepids, and onychodontids (Jarvik, 1948; Andrews, 1973). The rostral regions of dipnoans are very poorly known and canals pass anteriorly and ventrally off the ossified rostral region in most. Miles (1977) maintains that there is no demonstrable ethmoid commissure in dipnoans.

Among Actinopterygii, an antorbital commissure between supraorbital canals is unknown. All known actinopterygians with the exception of one Bear Gulch taxon, "worm fin," (Lowney, in press; Lowney, 1980) lack an extension of the supraorbital canal anteromesial to the narial openings. In "worm fin" the supraorbital canal passes mesial to the nares anterior to a junction with a lateral commissure presumed be the anterior lateral. This commissure courses between the nares to join the infraorbital canal at the beginning of the ethmoid commissure. A short, blind canal extending dorsally from the infraorbital canal anterior to the rim of the orbit is believed to be a portion of the posterior lateral commissure. In *Acipenser* (Jarvik, 1948; Jollie, 1980), the supraorbital canal ends at the level of the narial

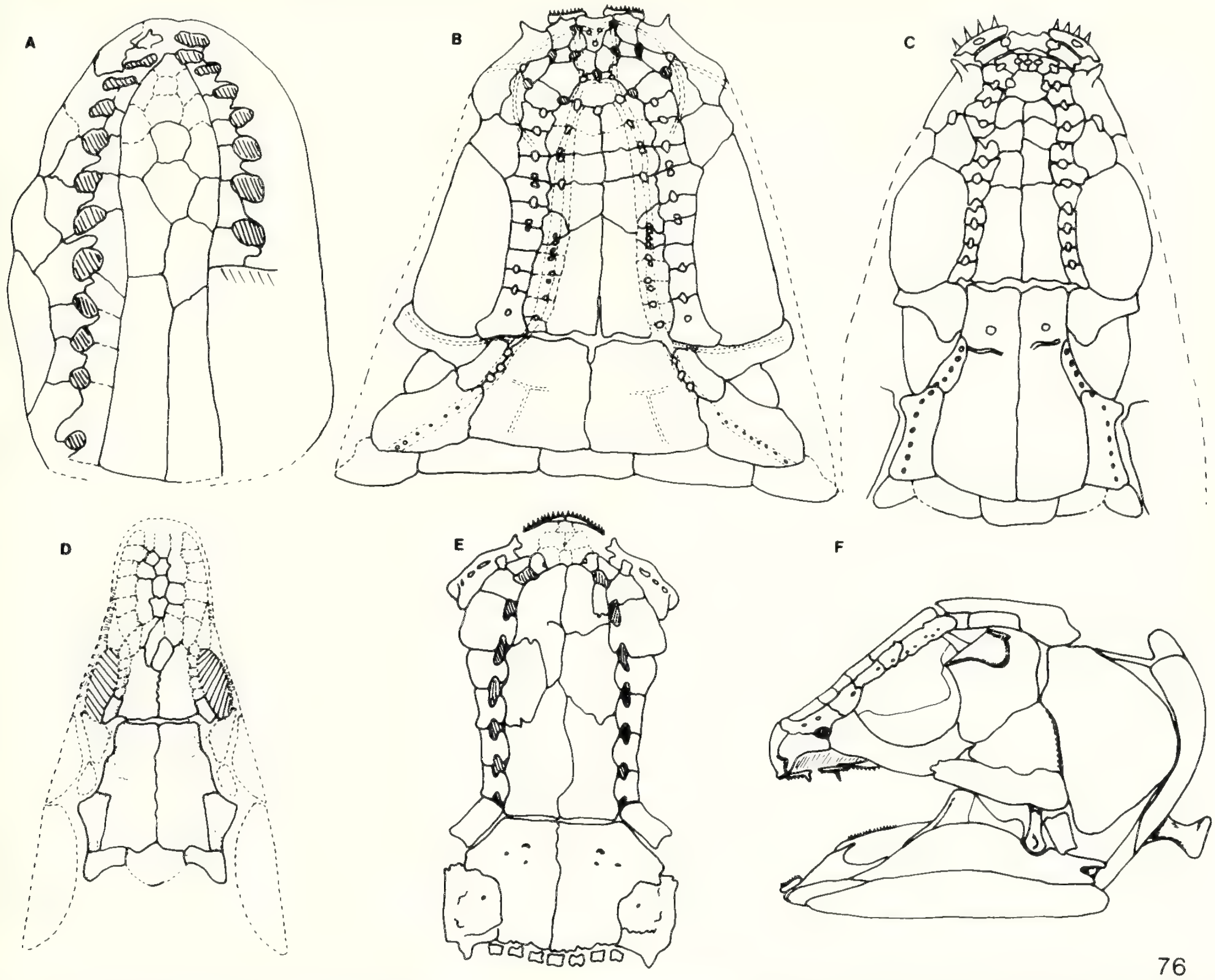

Fig. 76.—Sarcopterygian skulls. A) *Porolepis brevis*; B) *Osteolepis macrolepidotus*; C) *Dipterus valenciennesi*; D) *Holoptychius flemingi*; E) *Eusthenopteron foordi*; F) *Dipnorhynchus sussmilchii*. A, B, D, E, after Jarvik, 1972; C, F, after Westoll, 1949.

openings after giving off a ventrolateral branch that passes between the nares and ends blindly. The suprarostral row of nerve sacs has been interpreted (Jarvik, 1948:69) as a remnant of the anterior lateral commissure on the basis of its innervation. Among the teleosts, the canal between the narial openings (in the nasal bone) may communicate with the infraorbital canal anteriorly, near the ethmoid commissure as in *Elops* (Nybelin, 1967), as well as along the anterior border of the orbit in *Osteoglossum* (Taverne, 1977), strongly suggesting the homology of these canals to the anterior and posterior lateral commissures respectively. An ethmoid commissure is lacking in most teleosts, but is represented as a line of neuromasts in many percomorphs (Freihofer, 1978).

Postorbitally, the supraorbital canal of actinopterygians primitively continues virtually to the rear margin of the cranial roof without communication to the infraorbital or otic canals, although the transverse otic pit line in some Bear Gulch actinopterygians may completely span the gap (Lowney, in press). An anterior extension of the postorbital branch of the infraorbital canal in the position of the epibranchial line can be found in some Paleozoic actinopterygians and in one Bear Gulch taxon "long pelvic" (Lowney, in press) it is continuous between supraorbital and otic canals. There is no evidence to indicate whether this is the principal pathway by which connections between supraorbital and otic canals evolved in more derived actinopterygians, as the supposed epibranchial line is invariably found in a single, highly specialized anteriorly extended postorbital (dermosphenotic) bone. Among teleosts, the supraorbital canal may end blindly without communication with the otic canal (*Hiodon,* Taverne, 1977) or course directly into the otic line at the level of the transverse supraorbital commissure (*Osteoglossum,* Taverne, 1977). This level of difference within an order of teleosts requires that the primitive condition for the ancestry of the teleosts retain at least the genetic capacity to generate both pathways.

The infraorbital canal in coelacanths curves upward behind the orbit, intersects the jugal line and then courses dorsally as the postorbital line (Fig. 43). The jugal canal meets the preopercular canal in a T-shaped intersection in *Polyosteorhynchus* and *Rhabdoderma* (Figs. 4, 54A), relatively low on the cheek but dorsal and well posterior to the quadratojugal pit line. The preopercular canal extends dorsal to the intersection before ending, usually accompanied by a prominent pit. There is no dorsal communication with the otic canal. In the rhipidistians, the main canal of the cheek courses posteriorly and then ventrally to join the mandibular canal, and is usually associated with the quadratojugal pit line in the same manner as in the coelacanths. The canal thus seems to be composed of the jugal plus the ventral end of the preopercular canal, with no indication of dorsal portion of the preopercular canal (Fig. 76). One porolepiform, *Holoptychius flemingi* (Jarvik, 1972), displays a short ventral canal through the prespiracular bone suggestive of a possible dorsal connection between otic and preopercular canals (Fig. 76D), but no close association is developed. In dipnoans, adults display a pattern of lateral line canals in the cheek as in crossopterygians (Figs. 76C, F), but early embryonic stages of *Epiceratodus* reveal a vertical preopercular canal in contact with the otic canal dorsally (Greil, *in* Stensiö, 1947), ontogenetically reinforcing the hypothesis that the dorsal limb of the preopercular canal is phenotypically suppressed prior to or during the early evolution of Dipnoi and Crossopterygii.

The primitive condition in the Paleozoic actinopterygians is as in the model, where the vertically oriented preopercular canal communicates between the mandibular canal ventrally and the otic canal posterior to the postorbital intersection (Stensiö, 1947; Lowney, 1980). Among the Paleozoic actinopterygians, only *Phanerosteon* is known to retain a complete jugal canal as well as a strong remnant of the quadratojugal canal (Lowney, 1980). In many Paleozoic actinopterygians only a small pit line remains of the jugal (or supramaxillary) line, and a secondary connection between preopercular and postorbital canals is acquired ventral to the intersection of postorbital and otic lines (Moy-Thomas and Miles, 1971). The condition of the preopercular and postorbital canals in the teleosts conforms to that of the most primitive actinopterygians, although only an occasional pit line remains of the jugal canal. It should be mentioned that in both the Chondrichthyes and the Acanthodii (Stensiö, 1947) the preopercular and postorbital lines separately connect to the otic canal, and a canal interpretable as the jugal canal is present.

It must be concluded that the pattern of lateral line canals in the Osteichthyes corresponds closely in details to that of the model (Fig. 73), and is sufficiently conservative to provide a basis for judgements of primitiveness and of homologies.

The lateral line canals of the antorbital region of the hadronectoroidean coelacanths retain a more primitive condition than that known in any other osteichthyan. The condition of the supraorbital-otic canal area in the Bear Gulch hadronectoroid coelacanths is less primitive than that of either the most primitive known dipnoan or actinopterygian conditions. The pattern is clearly more primitive than either porolepiform, osteolepiform, or onychodontiform conditions. Further, the more derived coelacanths display a pattern convergent upon the osteolepoid condition, as well as that of the more derived dipnoans, but there is reason to suggest that the porolepoid condition represents a separate derivation. The canal pattern of the cheek of coelacanths is slightly more primitive than the ontogenetic expression of dipnoan and rhipidistian cheeks, approaching the primitive condition as expressed in the Paleozoic actinopterygians and present in the early ontogeny of the dipnoan *Epiceratodus.*

External Bones of the Head

The cranial osteology of coelacanths is the final ontogenetic expression of three apparently separate anatomical systems, the lateral line, the external "ornamental" skeleton, and the basal bones, interrelated through developmental processes that are still only poorly understood. It is clear that lateral line canal bones may ossify through the fusion of several bone primordia, each primarily associated with a neuromast (for example, Pehrson, 1947). It is also clear that lateral line canal bearing bones seem to be as subject to gross individual variation (Jarvik, 1948; Jollie, 1980; Parrington, 1949; Miles,

1977) as "anamestic" bones. Ontogenetic and phylogenetic pathways of the odontodes or odontode layers also coincide to a greater or lesser extent with those of the deeper mesodermal bone (*Hadronector*; see Lowney, 1980; Ørvig, 1975). Development of the bones of the skull additionally may be subject to modification in response to shifting mechanical stresses from genetically unrelated anatomical systems, a topic virtually unexplored in fish but actively explored elsewhere. Therefore, decisions on bone homologies and phylogenetic implications, when made without realization of the potential complexities of these factors, can prove quite misleading. The Bear Gulch coelacanths cast some new light upon the developmental aspects as well as the basic pattern of coelacanth osteology, and by extension into the basic interrelationships of the Osteichthyes.

Supraorbital canal bones.—The condition of the bones of the dorsal aspect of the head that most closely approximates the model of the primitive lateral lines is seen in *Dipnorhynchus sussmilchi* (Fig. 76F), where the supraorbital canal lies under the centers of the middle of three paired series of bones from the rostral region to the rear of the skull (the series Q, M, L, K, J3, of Westoll, 1949). The most mesial series of bones lacks a lateral line canal as far forward as can be resolved and contains only one large paired element, and the lateral series consists of apparently non-canal bearing supraorbitals followed by a series of four bones carrying the otic canal (the series 4, X, Y_1, Y_2 of Westoll). The smaller bones in each longitudinal series correspond to each other more or less precisely in transverse rows. Among the Hadronectoroidei, the general pattern consists of three longitudinal series from the anterior end to the rear margin of the skull. Anterior to the intracranial joint differences occur in that both the lateral and the central series participate in the pore system of the supraorbital canal (*Polyosteorhynchus, Allenypterus,* Fig. 75B), and that in all coelacanths there is an additional large element in the most mesial series anterior to the intracranial joint, the parietal. *Allenypterus* displays late ontogenetic fusion of the middle to the most mesial series, *Hadronector* shows fusion of elements of the lateral supraorbital series, and all other known coelacanths except *Euporosteus* (Fig. 75A) have only two series of longitudinal elements, the consolidation of middle and mesial series evidently taking place in early ontogeny.

All coelacanths display only two series of bones posterior to the intracranial joint, a derived condition. Further, the otic series, the supratemporal and tabular, consists of fewer bones than in *D. sussmilchi* and reduction of the supratemporal bone in the coelacanths results in either its elimination (*Latimeria*) or possibly fusion of the middle series in Dipnoi with the most mesial element (B_2 of Westoll).

Osteolepiformes and Onychodontiformes have only two series of elements, the supraorbital canal passing from the nasal series most anteriorly into the mesial element over the orbit, then laterally again postorbitally. The most posterior element in the middle series bears transverse and posterior pit lines, has been called the postparietal and seems to be comparable in detail with the postparietal of coelacanths. A non-canal bearing bone, the extratemporal, is found lateral to the tabular of *Osteolepis, Porolepis* and *Onychodus* (Andrews, 1973), that is not found in coelacanths. The one or two supraorbitals in Osteolepiformes lack canals.

The rostral region of *Holoptychius flemingi* consists of a large and variable number of bones in a mosaic relationship to each other (Fig. 76D), and a variable pattern of branching of the lateral line canals. Comparison of this region with other crossopterygians is made difficult because of bone growth and overgrowths of cosmine; both *Eusthenopteron* (Fig. 76E) and *Strunius* (Jessen, *in* Moy-Thomas and Miles, 1971) have relatively few, large bones in the same area, but the patterns seem to differ. Dipnoans as well generally have solidly ossified rostral areas, but *D. sussmilchi* (Miles, 1977) and *Uranolophus* (Denison, 1968) show traces of mosaic ossification in this region.

Accepting the concept that the basal gnathostome condition may be typified by an acanthodian-like state of many small dermal elements, the holoptychiid and dipnoan condition may represent the most primitive known in the Osteichthyes, although details are absent. Posterior to this region, however, although *Holoptychius* has several more supraorbital bones than any osteolepiform, neither *Holoptychius* nor *Porolepis* has a clear indication of either middle or lateral bone series except for the tabular and an extratemporal ossification. The supraorbital canal continues into the postparietal, and the otic canal is represented only by a short segment in the tabular.

The published actinopterygian condition is never seen to consist of more than two longitudinal series of bones, the supraorbital canal being associated with the mesial series; except in *Acipenser* where three series are present in the supraorbital region and the canal is generally associated with the middle series (Jollie, 1980; but see Jarvik, 1948, for variations). A large and variable number of bones are found in the rostral region, but not associated with lateral line canals. The signficance of the osteology of *Acipenser* is uncertain, but the pattern of bones of the supraorbital canal in published Actinopterygii is clearly derived relative to the coelacanths.

A pair of very small series of bones at the anterior end of the supraorbital canal of Hadronectoroidei seem to represent ossifications of the antorbital and the anterior lateral commissures. They may be equivalent to the frontonasals or tectals of *Eusthenopteron* (Fig. 76E) or some of the series of small elements in *H. flemingi* (Fig. 76D), and in turn to the anterior supraorbital canal elements in "worm fin" (Lowney, in press) among the Actinopterygii, but in no case can the requisite canals be demonstrated that would establish direct relationships. At present this condition among the coelacanths must be considered as primitive for all Osteichthyes. The loss of these canals and bones in the Coelacanthoidei, therefore, would constitute a set of derived states.

Anterior infraorbital canal bones.—The ethmoid commissure is carried in association with the rostral bone in known primitive coelacanths. It is felt that this small element and the associated canal are more likely to be missed in the specimens than to be absent from the species in which they have not been reported. The rostral of the hadronectoroids and *Rhabdoderma* separates the premaxillae in the midline, but is not toothed. *Holoptychius flemingi, Eusthenopteron,* and Onychodontiformes are reported to have a small median rostral, which does not separate the premaxillae in the midline. The ossified dipnoan anterior region is not comparable. A small, separate, canal carrying rostral bone, bearing teeth, is also considered the primitive condition in Paleozoic actinopterygians by Lowney (1980, in press), who has found no evidence for the previously reported "rostropremaxilloantorbital" of Gardiner (1963) in any actinopterygian. With the exception that the rostral of coelacanths does not bear teeth, the coelacanth and actinopterygian condition is considered primitive, without being able to evaluate the lungfish.

A series of anterolateral rostrals is present in Hadronectoroidei, followed by a prominent posterolateral rostral in all coelacanths. Reduction in numbers or elimination of the anterolateral rostrals would constitute a series of derived character states. The posterolateral rostral of all coelacanths has a distinctive morphology relating it not only to the infraorbital lateral line canal but to the (topographically) anterior naris, and indirectly to the presence or absence of choanae. There is a bone in *Holoptychius flemingi* closely resembling the posterolateral rostral (Fig. 76D), and there is a virtually identical bone in the Devonian Gogo onychodontid (Andrews, personal communication). No other known osteichthyans have a bone appearing in any way to be similar. The anterior portion of the infraorbital canal is supposedly carried in the premaxilla of all known rhipidistians, a clearly derived condition (Pehrson, 1947) relative to the coelacanths. Among actinopterygians, only the recent *Elops saurus* has separate anterolateral rostrals (Nybelin, 1956), whereas virtually all others carry the anterior portion of the infraorbital canal in a single antorbital bone that may represent the fusion of the coelacanth lateral rostrals, antorbital and anterior part of the lacrimojugal. The condition in most actinopterygians is derived relative to the coelacanth condition. In *Allenypterus, Hadronector,* and probably *Polyosteorhynchus,* there is evidence for a series of bones between the supraorbital canal series and the infraorbital canal series, associated with the posterior lateral commissure and the posterior pores of the rostral organ. The loss of these bones, and the loss or modification of the canal organs, would constitute derived states. The rhabdodermatids retain only the antorbital bone, whereas coelacanthids eliminate this element as well.

There are considered to be two external narial openings as a primitive condition in all Osteichthyes, although the position of the nasal capsule varies from ventral in dipnoans to ventrolateral in coelacanths and crossopterygians to dorsolateral in actinopterygians. From the standpoint of morphological and functional complexity, a secondary association between the flow across the olfactory membrane and flow of respiratory water into the mouth has arisen several times within the gnathostomes. The suggestion of Andrews (1973), therefore, that the absence of a choana in Onychodontiformes and Coelacanthiformes may be a secondary loss, may be the least parsimonious hypothesis. An objective position on this question, however, is difficult to state, just as is an objective position on a number of other critical distinguishing absences in the coelacanths such as cosmine, a maxilla, and a supraotic cavity (Miles, 1977).

A series of large median postrostral elements is found only in *Hadronector, Diplocercides,* and *Euporosteus* among coelacanths. In other coelacanths, a large element called the postrostral is associated with the anterior end of the frontonasal series and pores of the supraorbital canal (or antorbital commissure). It may be a fusion of several paired elements, thus not strictly homologous with that of *Hadronector.* There is very little basis for assignment of directionality to evolutionary trends in these elements aside from their reduction or absence in other coelacanths. Only *Holoptychius flemingi* shows bones in this area among crossopterygians, and it has four small bones (Jarvik, 1972); other crossopterygians and dipnoans do not reveal separate ossifications.

Actinopterygians generally have a single postrostral, that may fuse to the rostral in some lines, though *Cheirolepis* (Watson, 1925) is restored with two median postrostrals. It shall be assumed that the presence of several postrostrals is primitive and their absence a derived condition.

A premaxilla is apparently present in all osteichthyans, and is found in several different states among coelacanths. It may be justifiable to assume that a simple toothed strip, perhaps with a slight dorsal lamina, represents the primitive state, as in *Allenypterus,* and that emargination of the dorsal lamina and perforation of the dorsal lamina for a pore represent separately derived conditions. The latter state is confined to a small assemblage of Carboniferous forms assigned to the Rhabdodermatidae. Dipnoans have a vague dentigerous "upper lip" (Denison, 1968; Bernacsek, 1977) fused to the remainder of the snout region. Osteolepoids, porolepoids, and onychodontoids have a premaxilla fused to the anterior infraorbital canal as does *Polypterus,* where the condition has been demonstrated to be secondary (Pehrson, 1947). The primitive actinopterygian condition is that of a toothbearing element with a dorsal lamina, not associated with a canal or fused with any other bones and separated in the midline by a rostral (Lowney, in press). The actinopterygian and coelacanth conditions are equally primitive as far as the data permit evaluation.

Posterior infraorbital canal bones; bones of the cheek.—All known coelacanths carry the infraorbital canal around the orbit through two bones, the lacrimojugal and the postorbital. Osteolepiformes, Porolepiformes, and Onychodontiformes all have three bones in the series, the lacrimal and jugal being separate ossifications. *Dipnorhynchus* has five bones, *Dipterus valenciennesi* has five or six bones, and most Paleozoic actinopterygians have two bones that do not correspond topographically to the coelacanth elements. Modern teleosts and two Bear Gulch actinopterygians have five or more elements. While there is no reason to agree upon a primitive number of elements in the series, the number apparently was higher than the two found in coelacanths.

The preopercular canal of *Rhabdoderma* and *Polyosteorhynchus,* among other coelacanths, courses through two bones between the mandible and the intersection with the jugal canal, the preoperculum and squamosal, as may the canal of *Nesides heiligenstockiensis* (Jessen, 1973). This is interpreted on present evidence as being the primitive condition for the order. Alternatively derived conditions include the reduction of the preoperculum with capture of the canal by the quadratojugal in *Whitea* (Lehman, 1952), the apparent elimination of a ventral bone in the series in "*Diplurus*" (Schaeffer, 1952), or the reduction of one or both of the bones to thin osseous tubes as in *Coelacanthus granulatus* (Schaumberg, 1978). The osteolepoids are similar to the coelacanths in number and position of the bones and canals. The Porolepiformes have three bones in the preopercular-jugal canal series, and no indicators of where, if at all, the two canals might have joined (see Stensiö, 1947). Further, *Holoptychius flemingi* is credited with a small dorsal branch of a canal in the prespiracular bone (Fig. 76D). There are four or five bones of the preopercular canal in early Dipnoi (Westoll, 1949; Miles, 1977). Among the Actinopterygii, there are two bones that carry the canal between mandible and otic canal, occasionally a third, equivalent to the postsubmandibular of Porolepiformes (Lowney, in press; Lund, in manuscript) and indications of a complete mandibular operculum dorsal to the articular. The jugal canal, although complete in only one Bear Gulch actinopterygian, *Phanerosteon,* crosses an additional bone between the preoperculum and the infraorbital line. There is therefore, evidence that at least four bones may have been primitively involved in the preopercular and jugal canals in the actinopterygian and dipnoan conditions, reduced somewhat in the coelacanths. There is also evidence for a complete mandibular operculum as the primitive osteichthyan condition. The pathways and phenotypic expressions of the lateral line canals of the cheek are complex and should not be considered as a single character state.

The Porolepiformes and *Dipnorhynchus* have four additional bones in the cheek, the two called the prespiracular and quadratojugal in porolepoids not necessarily corresponding to bones in the cheek of lungfish. The coelacanths have elements that may reasonably be called prespiracular and quadratojugal but lack any other cheek bones; *Osteolepis* lacks a prespiracular, as may *Eusthenopteron,* which is a derived state relative to dipnoans, porolepiformes and coelacanths. The prespiracular and ventral preoperculum (postsubmandibular) are reasonably stated to be derivatives of the dorsal half of the mandibular operculum (Jarvik, 1963). No dipnoan has a spiracle, nor a prespiracular, but several taxonomic groups among the Bear Gulch actinopterygians retain various stages in the reduction of the dorsal part of the mandibular operculum to the relatively derived stage present in porolepoids.

The mandibular lateral line canal in coelacanths is carried in two bones, the angular and the "splenial," or anterior infradentary. *Dipnorhynchus* among the dipnoans, as well as *Holoptychius* and *Eusthenopteron,* carry the mandibular canal on a chain of infradentaries, a more primitive state than the coelacanth condition. Actinopterygians are separately derived in carrying the canal on two bones, the largest of which is the dentary (Lowney, 1980), the sole anterior lateral bone of the lower jaw.

The dentary is a small element at the anterodorsal margin of the lower jaw in most coelacanths. It is proportionately longer in *Polyosteorhynchus* and *Lochmocercus,* and even more so in young individuals of the former genus. The occlusal line of the dentary continues smoothly back to the coronoid eminence of the angular in these two forms, a condition that corresponds with the occlusal line of other osteichthyans and can be accepted as primitive. Miles (1977) also convincingly argues that a longer dentary can be accepted as primitive for both coelacanths and dipnoans. The anterior angular diastema in the occlusal line of most later coelacanths (*Caridosuctor,* Fig. 21), and the strong angulation between the dentary-splenial and the angular portions of the jaw are considered derived conditions, the latter of which seems to have been very variable among coelacanths (Schaeffer, 1952). The diastema may be associated with the development of the maxillolabial ligament in *Latimeria* (Millot and Anthony, 1958). There seems to always be a complete series of vaguely defined coronoid elements from an adsymphysial plate to the uniquely enlarged coronoid of coelacanths, although the angle, dentition and relationships of the coelacanth element here termed precoronoid is quite varied. The presence of this series seems to be primitive for osteichthyes (Miles, 1977), although the coelacanth coronoid is a uniquely derived modification. The supposedly triangular coronoid mentioned in some coelacanths is probably an artifact of observation, although coronoids do differ in shape of the dorsal edge, position and dentition.

No coelacanth has a maxilla. Coelacanths share this condition only with dipnoans. It is not possible to determine the primitive state of the posterodorsal margin of the mouth on the basis of objective criteria for coelacanths, but there seems to be some reason to believe that the condition is primitive for dipnoans. It may be presumed, for argument, that the lengths of the dentary and maxilla closely correlate for functional reasons in primitive rhipidistians and actinopterygians. A relatively long dentary in occlusal line with the enlarged angular seems to be primitive for coelacanths (see above). This suggests that very different stress distributions were present in the most primitive coelacanths like *Lochmocercus* and *Polyosteorhynchus* and strongly suggests derivation from an ancestor that transferred biting forces along the lateral aspect of the jaw as well as weaker forces along the prearticular. We feel that the lack of a maxilla in coelacanths is a uniquely derived feature.

The palates of coelacanths are all very similar in osteology and articulation. There is a well developed autopalatine, anteroventrally fringed with tooth plates in the position of a dermopalatine. The vaguely defined dermopalatine tooth patches form a continuous line of fine teeth between vomers anteromesially and the thin ectopterygoid along the lateral edge of the endopterygoid, the principal bone of the palate. The absence of a well defined dermopalatine may be a primitive condition. The posterodorsally placed metapterygoid (epipterygoid) articulates with a well developed antotic process in all known coelacanths, although the antotic of hadronectoroids may project as far laterally as posteriorly to the intracranial joint. There is no evidence for a basipterygoid process in any coelacanth but Diplocercides (Bjerring, 1973); the absence of this articulation is considered a derived character among coelacanths (Andrews, 1977).

As far as can be determined, no coelacanth has well developed pharynogobranchial elements or unspecialized epibranchial elements. They are thus uniquely derived among the major taxonomic groups of gnathostomes in this regard.

The primitive condition of the opercular series among known coelacanths is to have both an operculum and a suboperculum, but to lack a branchiostegal series between the suboperculum and the gular plate, as in Hadronectoroidei. No other coelacanths have a bone with the distinctive morphological relationship to the operculum that a suboperculum must have except perhaps *Nesides*? *heiligenstockensis* (Jessen, 1973). All Coelacanthoidei are derived in this character state. All Coelacanthiformes are derived in the lack of branchiostegal rays, a median gular or submandibular bones relative to dipnoans and crossopterygians. Dipnoans share with coelacanths a marked reduction in the branchiostegal series (Miles, 1977). The actinopterygians lack a submandibular series related to the lower jaw, and only occasionally have lateral gulars; the former is derived state, whereas the second is primitive in relation to the remainder of the Osteichthyes (Lowney, 1980).

Shoulder Girdle

A bony attachment of the dorsal end of the shoulder girdle to the skull roof is rarely well preserved among coelacanths and seems to be absent in most, a presumably derived condition relative to the remainder of the Osteichthyes. There is a suggestion of a stout, anteriorly inclined element in *Diplocercides* and *Lochmocercus* that may have fulfilled this function in a manner similar to that of the remaining crossopterygians; this is considered here as primitive. Vertical, spike-like anocleithra as in *Polyosteorhynchus,* short, blunt vertical elements as in the Rhabdodermatidae, or S-shaped elements as in *Allenypterus* and *Hadronector,* none of which have a bony anocleithral spur to the braincase, are considered as derived conditions. *Macropoma* (Fig. 75F), however, has both an anterior process and a vertical process, which may be a secondary condition.

Extended anteroventral processes of the cleithrum and posterodorsal processes of the clavicles, associated with a loose, large extracleithrum are the derived condition among coelacanths, as found in *Allenypterus* and Rhabdodermatidae. The presence of the extracleithrum itself may be very difficult to demonstrate if all elements of the shoulder girdle are tightly associated, as in *Lochmocercus,* primitive dipnoans, crossopterygians and actinopterygians. The structure and function of osteichthyan shoulder girdles needs considerably more analysis before the details can be used in any evolutionary schemes.

No coelacanth has an interclavicle, a condition that agrees with that of onychodontoids (Andrews, personal communication) and actinopterygians. Primitive dipnoans, porolepoids and osteolepoids, have an interclavicle (Andrews, 1977), a condition that has been interpreted as primitive (Andrews, 1977).

Postcranial Skeleton

All well preserved coelacanths share the uniquely derived ossified swim bladder wall.

All well preserved coelacanths have numerous sclerotics, a character they share in common with a diverse assortment of totally unrelated gnathostomes (Miles, 1977).

Pelvic girdles are primitively located near the rear of the peritoneal cavity, as in *Allenypterus* and other osteichthyans. The derived condition as found in other Hadronectoroidei is a midabdominal location of the pelvics, while this condition is complicated in the Coelacanthoidei by the rearward inclination of the first haemals and freeing of the anal fin support from the first haemals. The pelvic plates are primitively simple and triangular (*Allenypterus*), and secondarily quadrangular (*Lochmocercus*) or elongate (*Polyosteorhynchus*) plates not articulating across the ventral midline, as in other osteichthyans (Rosen et al., 1981). *Hadronector* shares with the Rhabdodermatidae and some other coelacanths the more highly derived condition (Figs. 35, 74). *Laugia* and *Allenypterus* have linked the pelvic girdle to the shoulder girdle by entirely different specializations. The pelvic plates of crossopterygians and dipnoans are poorly represented, but separate, triangular plates in osteolepoids (Andrews and Westoll, 1970*a*, 1970*b*) are found. In dipnoans there is a single, median plate (Miles, 1977), while the minimal data available for actinopterygians also indicate paired, simple triangular plates (Lowney, 1980).

The paired fins of the Bear Gulch coelacanths add no useful information to what is already known. Both pectoral and pelvic fins are lobed, borne upon an endoskeletal axis articulated to the scapulocoracoid by one radial, branched distally, and externally scaled and muscularized (Andrews and Westoll, 1970*a,* 1970*b*). They share this character with all known Crossopterygii (except that the porolepiform axis is presumably secondarily unbranched; Andrews, 1973) as well as with dipnoans. They differ strongly from the actinopterygian paired fin supports, which consist of a single row of segmental radials. It is presumed that the actinopterygian condition is primitive (Goodrich, 1930).

The first dorsal fin support of coelacanths consists of a basal plate articulating directly, as far as is known, with serially arranged fin rays. The first dorsal fin support of the known crossopterygians (Andrews and Westoll, 1970*a*) has at least one distal row of radials, while dipnoans and actinopterygians primitively share a segmentally arranged median fin supported by rows of supraneurals (epineurals), baseosts, and axonosts (Obruchev, 1967; Lowney, 1980).

The second dorsal fin of *Latimeria* is supported by a basal plate with a long anterior process, a thin ventral process and a posterior articulation with branching, jointed radials (Andrews, 1973). In hadronectoroids and *D. huxleyi* there is no anterior process and the plate itself is rounded and almost directly under the fin. There are no preserved distal elements in fossil coelacanths. In *Eusthenopteron* and osteolepids, there is a single, slightly distally expanded proximal element followed by two series of more distal radials. In Porolepiformes there is a large plate serially homologous with epineurals, followed by two to three serial rows of radials distally (Andrews and Westoll, 1970*a*, 1970*b*). It seems most conservative to accept three rows of elements distal to the neural spines as primitive, and consider the porolepiform condition secondarily modified, as are the paired fins.

The anal fin supports of coelacanths primitively consist of a single basal plate supported dorsally from the first two haemal spines, as in Hadronectoroidei. *D. huxleyi* shows an anterior shift of the distal end of a basal plate shaped very much like that of the osteolepoids, while retaining the proximal support upon the haemal spines; Rhabdodermatidae show, as far as the elements ossify, a simple rod in the ventral body wall, while Coelacanthidae have accessory processes on the free ventral anal support (Schaeffer, 1941). The anal fin support of other Crossopterygii consists of a narrow plate plus two series of distal radials, that of the osteolepoids supported below the first haemals while that of the porolepoids is secondarily located behind the first complete haemal. Anal fins of dipnoans and Actinopterygii are supported upon serially arranged infrahaemals, baseosts and axonosts, considered to be the primitive condition. It should be noted that with the exception of the Porolepiformes second dorsal plate, the median fin supports of all crossopterygians are homologous with single epineural or infrahaemal elements, in strong contrast to the dipnoan and actinopterygian conditions.

All coelacanths have the neural arches and spines fused into a single, median structure. In contrast, the most anterior trunk neural elements in osteolepoid and porolepoid fish may be unpaired (Andrews and Westoll, 1970*a*, 1970*b*), and there are suggestions that the anterior neural elements may not have fused in some dipnoans (Obruchev, 1967). The primitive actinopterygian condition is paired, unfused neural arches and spines (Lowney, 1980), a condition that is also primitive for the chondrichthyan axial skeleton. A clear series of specialized cervical neural arches, as seen in all Bear Gulch coelacanths, is similar to the condition in *Latimeria* (Andrews, 1977). Preservational deficits make the cervical region an inaccessible character in most species.

The external shape of the tail of coelacanths is diphycercal, with an extended caudal lobe and tuft. The terminal caudal lobe and tuft are present as an adult character in Onychodontiformes, other juvenile crossopterygians (Schultze, 1973; *Miguashaia* has no unique coelacanth characters, either illustrated, described, or implied), all Bear Gulch actinopterygians in which preservation allows the determination (Lowney, 1980), juvenile *Lepisosteus* (Schultze, 1973), and the crank shaped tail of developing teleosts (Westoll, personal communication), and therefore must be considered primitive for the Osteichthyes irrespective of the angle of the body axis or the shape of the caudal fin itself. The shape of the caudal fin, whether rounded, elliptical, or square cut, is a highly adaptive character (Lund et al., in press; Dicanzio, in press) related to acceleration, aspect ratio, and drag (Alexander, 1973), and cannot be used in analysis of relationships among distantly related and ecologically isolated fish. Of considerably more pertinence are two other features, heterocercality and the symmetry of internal structure. On the symmetry of internal structure, endoskeletal supports of the caudal fin are more or less symmetrical across the axis in coelacanths, with as great an epichordal component as a hypochordal component. There is one row of well developed endoskeletal supports distal to the neural and haemal spines in all, including the asymmetrical and highly derived *Allenypterus.* In all crossopterygians where the endoskeleton is known, a series of supports distal to the axial spines can be found only hypochordally, although there are precaudal epineurals in porolepoids (Andrews and Westoll, 1970*a*), a derived condition. The presence of free caudal epineurals would indicate that the diphycercal condition is primitive, as in coelacanths, whereas their absence would indicate secondary diphycercality, as in *Eusthenopteron* (Obruchev, 1967). The endoskeletal supports for the caudal fin of Onychodontiformes are unknown, but there seem to be no substantive differences between the condition in *Strunius* (Andrews, 1973) and that in coelacanths. Dipnoi are said to have up to three rows of distal radialia (Obruchev, 1967), although details are lacking in most lungfish. There is a single series of epichordal radials anterior to the caudal fin in occasional teleosts (J. Dooley, personal communication), although none are reported in the fossil record. Distal radials of the hypochordal lobe of Actinopterygii are rare, quite reduced and not continuous to the end of the haemal series (Lowney, 1980). It has been accepted virtually without question that the heterocercal tail is primitive for bony fish (Andrews, 1973, for instance) and probably for gnathostomes, simply because of its prevalence (Romer, 1966), but this hypothesis introduces difficult evolutionary problems with regard to the internal structure of the tail. Clearly, in all cases of heterocercal tails, the distal epichordal radial series is absent or unossified. It is very unlikely to expect that distal radials would reappear in a secondarily diphycercal tail separated from influence of an also secondarily elongate dorsal fin, and indeed they do not. One is therefore forced to accept either that the diphycercal tail with unreduced epichordal components is primitive, and heterocercal tails arose several times in parallel, or that distal epichordal elements arose anew in some, but not all, diphycercal tails. Considerations of the Chondrichthyes in this situation do not clarify or strengthen the primitiveness of the heterocercal tail and suggest that the primitive condition of the chondrichthyan caudal is also internally symmetrical. While there is presently no elegant solution to this question, we assume that the coelacanth condition is derived relative to reputed dipnoans with more than one row of distal elements, and primitive relative to the crossopterygians as well as the actinopterygians.

A greater number of fin rays than endoskeletal supports is said to be primitive for coelacanths (Stensiö, 1937), while the presence of branched fin rays is said to be primitive for crossopterygians (Andrews, 1973). The fin rays of Dipnoi are not bony (Obruchev, 1967) but cartilaginous, while the fin rays of actinopterygians are bony but do not necessarily show any clear relationship between branching and any evolutionary tendencies (Lowney, 1980). The primitive coelacanth condition of fin ray numbers in the median and paired fins is derived relative both to the primitive condition in Crossopterygii and Actinopterygii, whereas the dipnoan condition appears to be a separately derived condition, from a crossopterygian-like condition (Denison, 1968).

All coelacanth scales are cycloid and ornamented with lines of enameloid on the posterior field, also a derived condition relative to the apparent primitive condition of other Osteichthyes. The absence of cosmine in coelacanths and actinopterygians is troublesome; Miles (1977) assumes for simplicity that the presence of cosmine is a shared, derived character among primitive crossopterygians and dipnoans, its absence primitive in coelacanths and actinopterygians. There seems to be little firm ground for a decision on this character in light of the trends among coelacanths for reduction of ornamentation and the separate origin, somewhere within the coelacanths, of a unique sensory system, the rostral organ, that may imply divergent sensory specializations among the early Osteichthyes.

INTERRELATIONSHIPS OF THE GROUPS

It is plausible to draw conclusions about the directionality of many characters among the coelacanths from the foregoing comparisons—several of these are embodied in Table 7. Several features of this comparison however are made difficult by the absence of relevant information among published accounts of many coelacanths. The resultant scheme of possible relationships is not aided by the observation that the Bear Gulch coelacanths, while divergent from even the Devonian Diplocercidae, are collectively more primitive in all useful character states than all other known coelacanths. The resultant scheme of relationships thus is a series of levels of change, or grades of evolution, in which there are virtually no conclusive connecting links between grades. Even within the Hadronectoroidei it is not possible to demonstrate any single preferable grouping of interrelationships or ordering in a single most parsimonious scheme.

Among the Devonian and Carboniferous coelacanths for which even a modicum of useful information is available, it is only possible to say that

Table 7.—*Comparisons of character states among coelacanths. Abbreviations: Am,* Allenypterus, *Ps,* Polyosteorhynchus*; La,* Lochmocercus*; Hd,* Hadronector*; C-R, Rhabdodermatidae; D,* Diplocercides *(after Stensiö, 1937); E,* Euporosteus *(Stensiö, 1937); Du,* Dumfregia*; Cg,* Coelacanthus granulatus *(Moy-Thomas and Westoll, 1936, Schaumberg, 1978); W,* Whitea *(Lehman, 1952); Un,* Undina *(from Schaeffer, 1941, 1952); M,* Macropoma *(Watson, 1921); Ax,* Axelia, Mylacanthus, Scleracanthus *(Stensiö, 1921); Di,* Diplurus *(Schaeffer, 1952); L,* Latimeria *(Millot and Anthony, 1958);* D^{1-n}*, derived character states 1 through n, usually implying a continuum;* D^9*, separately derived state, P, primitive. Refer to text for discussion.*

Characters	Am	Ps	La	Hd	C-R	D	E	Du	Cg	W	Un	M	Ax	Di	L
Premaxilla	P	D^1	?	D^1	D^9	?	?	?	P	D^2	P?	D^2	D^2	P?	P?
Mesial supraorbital	P	P	?	D	P	P	P	D	D	D	D	D	D	D	D
Lateral supraorbital	D^1	P	D^2	D^9	D^2	D^2	P	D^2	D^2	D^2	D^2	D^2	D^2	D^2	D^2
Anterolateral rostral	P	P	?	P	D^1	?	?	?	?	?	?	?	?	?	P?
Antorbital	P	P	P	P	P	P	?	P	D	P	P?	D	D	D	D
Extra snout series	P	P	?	D^1	D^2	?	?	?	D^2	D^2	D^2	D^2	?	D^2	D^2
Cheek bones	P	P	P	P	P	D	?	?	D	D	D	D	?	D	D
Supratemporal & canal	P	P	D^1	D^1	D^1	D^9	?	?	D^9	D^9	?	P?	?	D^2	D^2
Extrascapulars	P	D^9	P	D^9	P	D^9	?	?	D^1	P	P	D^2	?	D^2	D^2
Dentary	D	P	P	D	D	D	?	?	D	D	P	D	?	D	D
Basipterygoid process	D	D	D	D	D	P	?	?	D	D	D	?	?	D	D
Anocleithrum	D^9	D^1	P	D^9	D^2	P?	?	?	P	D	?	D^9	?	D^1	D^1
First dorsal plate	D^1	D^2	D^2	D^2	D^1	?	?	D^1	D^2	?	D^2	D^2	?	D^2	D^2
Second dorsal plate	P	P	P	P	D	?	?	P	D	?	D	?	?	D	D
Pelvic plate	P	P	P	D^2	D^2	?	?	D^1	D^2	D^2	D^1	?	?	D^2	D^3
Anal plate	P	P	?	P	D^2	?	?	D^1	D^2	?	D^2	?	?	D^3	D^3
Caudal rays	P	D	P	D	D	P	?	D	D	D	D	?	?	D	D

there were two concurrent major groupings. The Coelacanthoidei, represented by the Devonian Diplocercidae, were structurally more derived in most known characters than the Hadronectoroidei, represented by holomorphs from the Namurian Bear Gulch limestone and *Coelacanthopis.* The Devonian *Euporosteus* is known from one isolated ethmosphenoid that may best be assigned provisionally to the Hadronectoroidei on the basis of the multiple series of bones (Fig. 75A). Among other forms assigned to the Coelacanthiformes, *Miguashaia* (Schultze, 1973), as previously discussed, is not a coelacanth. *Chagrinia* (Schaeffer, 1962) shows no diagnostic characters, nor does the unique specimen of "*Coelacanthus*" *welleri* Eastman (1908). Neither the specific nor generic assignment of *Rhabdoderma exiguum* have been confirmed by osteological studies. The putative genus *Synaptotylus* (Echols, 1963) has been in part commented upon by Forey (1981), and his comments on the jaw suspensorium are well founded. The squamosal of "*Synaptotylus*" as illustrated by Echols is extremely close to that of *R. elegans* (Figs. 6–9), but neither this character or any other enable systematic placement to genus to be made. Little more can be said about the British Carboniferous coelacanths assigned to *Rhabdoderma* by Forey (1981) than discussed earlier in this paper; they may be Rhabdodermatidae *sensu stricto* but are not *R. elegans.*

To review the details of Mesozoic coelacanths given in Table 7 would only serve to detail how little is actually known about them. Perhaps the only derived character present in the Bear Gulch coelacanths, including *Caridosuctor,* not present or noticed in other Coelacanthoidei, is that of the cervical neural arch series. Functionally, the cervicals are strongly correlated with the ability to move the oticooccipital moiety of the braincase upon the axis during feeding (Lund et al., in press) and their absence in some species may imply nothing more than subtle differences in feeding mechanism. There is little justification for placing heavy weight on a character where the state of it is unknown in most members of one of the groups.

INTERRELATIONSHIPS OF COELACANTHIFORMES

Among the coelacanths the premaxilla may occur as a toothed strip bearing an undistinguished dorsal lamina, as in *Allenypterus,* which is taken as the primitive condition. Emargination of the dorsal lamina for pores, apparently associated either with the ethmoid commissure or with the rostral organ, is considered a derived character, whereas the perforation of the dorsal lamina for a large pore most likely associated with the rostral organ, as seen in *Caridosuctor* and *Rhabdoderma*, is considered a separately derived state. The thin toothed strip found in *Coelacanthus, Undina*, "*Diplurus*," and *Latimeria* may constitute retention or modification from a primitive condition. In *Whitea* (Lehman, 1952) and *Macropoma* (Watson, 1921), the premaxilla has not been found as a separate element, but is reported fused or tightly sutured to the other elements of the rostral region, probably a secondarily derived condition. The two rows of anterior supraorbitals in *Allenypterus, Polyosteorhynchus, Hadronector*, probably in *Euporosteus*, and restored in *Diplocercides*, is considered the primitive state. All other known coelacanths are derived in having a single row of supraorbitals anterior to the orbit. Posterior to the antorbital, *Polyosteorhynchus* maintains two rows of supraorbitals at least to the ontogenetic stages known, *Allenypterus* fuses the mesial row to the medial series in ontogeny, and *Hadronector* fuses the lateral supraorbitals into two elements while retaining some semblance of the mesial series. These are alternative variations upon the primitive condition, which is seen most clearly in *Polyosteorhynchus*. All other coelacanths are derived in having only a single row of supraorbital bones. It should be noted that while in *Allenypterus* the posterior two lateral supraorbitals fuse, there is no significant projection of the supraorbital series posterior to the intracranial joint in either it or *Hadronector* and only slight posterior projection in *Polyosteorhynchus*, probably reflecting the lateral extent of the antotic process. In other coelacanths there is a distinct projection of the last supraorbital posterior to the intracranial joint (Fig. 75).

The presence of several anterolateral rostrals is considered primitive, the reduction to one element, as in *Caridosuctor* and *Rhabdoderma* is derived, and the elimination of this element, where this can be established, is further derived. The presence of a series of bones between the supraorbital and infraorbital canals, extending back to and including the antorbital, is considered primitive for coelacanths, its reduction in *Hadronector* and restriction to a single antorbital in Rhabdodermatidae, *D. huxleyi, Diplocercides*, and *Whitea* a first order derived character, whereas its elimination in *Coelacanthus* and other coelacanths constitutes a secondary derived condition.

Primitively in known coelacanths there is a completely bone covered cheek composed of five tightly abutting or overlapping elements, plus a single lacrimojugal. This is found in all Bear Gulch coelacanths and *Rhabdoderma elegans. Whitea* contains five bones in relatively loose association, with the prespiracular and preoperculum reduced, whereas other coelacanths are reported to have only four bones in various states of reduction, all derivable from a *Whitea*-like state and ultimately from the primitive condition.

A suboperculum, clearly provable by its association with the operculum, is present only in Hadronectoroidei and is absent in all other known coelacanths. The latter condition is derived. The operculum articulates with the tabular in *Allenypterus, Caridosuctor* (but not *Rhabdoderma*), and *Spermatodus* (Westoll, 1939), almost undoubtedly constituting separate derivations in each genus. There apparently were strong selective pressures for this association, possibly linked to the use of opercular pumping in the feeding mechanism (Lund et al., in press).

The otic canal passes between postparietal and supratemporal in *Allenypterus* and apparently in *Polyosteorhynchus*, and in no other known coelacanths. The otic canal occurs within the supratemporal in *Hadronector* and Rhabdodermatidae, and apparently in *Lochmocercus*, and in *Latimeria* passes lateral to the postparietal unaccompanied by bone, as seems to be the case in "*Diplurus*" (Fig. 75E). It has been restored as passing through the lateral margin of the postparietal in *Diplocercides, Coelacanthus granulatus, Whitea*, and *Mawsonia* (Wenz, 1975). While there is little basis for judgment on which condition is primitive, the presence of a supratemporal is primitive, and by extension to the primitive dipnoan condition the path of the otic canal through the most lateral bone series would also constitute the primitive condition. Thus, reduction to elimination of the supratemporal would be one pathway (*Rhabdoderma*-"*Diplurus*"-*Latimeria*) and a relative mesial movement of the canal an alternate derivation (*Polyosteorhynchus-Diplocercides-Coelacanthus*). The utility of this character, however, is severely strained by the speculative nature of the path of the canal in many cases.

The palates of coelacanths seem to vary only in proportions and in patterns of denticulation. Sutures between endopterygoid and metapterygoid generally tend to be either loose or obscured by overlying bone, but the quadrate is virtually never isolated by sutures. The ectopterygoid is present in all

Hadronectoroidei and Rhabdodermatidae, as a thin element that always extends to the level of the middle of the coronoid. There is a thin line of tooth bearing bones, "dermopalatine," under the well developed autopalatine that forms a continuous line between the vomerine teeth anteriorly and ectopterygoid teeth posteriorly. There is no evidence in any Bear Gulch coelacanth for a basipterygoid process, but braincases are not ossified in one piece and are generally collapsed, so evidence in this regard is weak indeed. In terms of braincase, and presumably absent basipterygoid process, the Bear Gulch coelacanths and all others are derived relative to *Diplocercides.*

The lower jaws of most coelacanths are very similar; the characteristic high coronoid, in tight association with the anterior edge of the quadratojugal, marking the corner of the mouth as in *Latimeria. Lochmocercus* and *Polyosteorhynchus* are primitive relative to all other coelacanths in lacking a distinct angular diastema, or, expressing the same appearance differently, in having relatively large dentaries on a more or less continuous occlusal line with the angular. In both cases the dorsal margin of the dentary is mesially inset, indicating with the coronoid that there may have been fleshy lips in these species as well. *Lochmocercus* also bears a prominent marginal dentition along the dentary, that can also be considered as primitive among coelacanths.

The extrascapular bones are here considered as all bones bearing the occipital commissure from its intersection with the head canal. As far as is known the primitive number of extrascapulars in coelacanths, and in dipnoans, seems to be five, rather than the three that are primitive for known crossopterygians (Andrews, 1973) or actinopterygians (Lowney, 1980). If this position is taken, *Allenypterus, Lochmocercus,* Rhabdodermatidae, and *Whitea* could be considered primitive, although in the case of *Rhabdoderma* and *Whitea* posterior extension of the tabular may have obscured the relationships. Thus, either fewer extrascapulars, as in *Polyosteorhynchus* and *Hadronector,* or more, as is the case in *Coelacanthus granulatus,* "*Diplurus,*" *Latimeria,* or *Undina* would potentially be alternate derivations in the absence of convergence. The posttemporal is difficult to detect in many coelacanths because of great reduction in thickness and size, but *Allenypterus* has a posttemporal, albeit small and thin, whereas *Hadronector* and *Polyosteorhynchus* have somewhat more evident posttemporals. If a posttemporal is indeed present in Rhabdodermatidae, it is very small and thin, and does not clearly show a lateral line canal. The evidence for postemporals in most other coelacanths is dubious.

A stout anocleithrum fixed to the skull can be presumed to be primitive. *Lochmocercus* may have this condition, *Macropoma* has it, and as far as can be established, no other coelacanths are primitive in this regard. All others show some reduction of the anocleithrum. The extracleithrum is spotty in its occurrence; preservational factors and functional integration of the clavicle and cleithrum, a primitive condition, tend to obscure its detection. A tightly integrated clavicle and cleithrum, as seen in *Lochmocercus* and *Polyosteorhynchus* (both of which show posteriorly projecting scapulocoracoid ossifications) contrasts with the somewhat looser association seen in *Hadronector* and the highly mobile three bone shoulder girdle of *Allenypterus* and the Rhabdodermatidae, the most derived state. *Diplocercides* and *Diplurus* have relatively tight associations between clavicles and cleithrum, whereas the remainder of the coelacanths seem to have a more mobile arrangement.

The second dorsal fin plates of Hadronectoroidei and *D. huxleyi* are primitive rounded plates with no significant posterodorsal articular facet. Rhabdodermatidae share with all other known coelacanths the derived condition. "*Diplurus,*" *Undina,* and *Latimeria* show further derivation in the extreme thinness of the anterodorsal process and in the lowering of several neural spines to either side of the ventral process.

The first dorsal plate rarely shows any ventral processes that suggest fusion from several baseosts. This relatively primitive condition is seen in *Polyosteorhynchus, Caridosuctor,* and *Undina,* the remaining coelacanths having a uniform ventral margin.

The pelvic plates of *Allenypterus, Lochmocercus,* and *Polyosteorhynchus* are primitively simple, triangular to quadrangular elements lacking significant surficial bone and not bearing a posteromesial articulatory process. The pelvic plates of *D. huxleyi* and *Undina* are thin, elongate structures with weak posteromesial processes at best, whereas those of *Hadronector,* the Rhabdodermatidae, *Coelacanthus granulatus,* "*Diplurus,*" and *Latimeria* bear strong articular processes. The pelvic plates of *Laugia* are highly specialized structures. The rhabdodermatid pelvics differ from the coelacanthid condition in having anterolateral rather than anteromesial processes.

The primitive condition of the anal fin support is seen in Hadronectoroidei, where a simple, rounded to elongate basal plate is supported upon a thin stem against the first haemal spine. In *D. huxleyi,* the plate is anteriorly inclined and expanded along its long axis but still braced against the haemal spine. The rhabdodermatid condition is a simple, rarely ossified rod. The anal supports of "*Diplurus*" and *Latimeria* are best described as reclining V's lying free in the ventral body wall, a highly derived condition.

The primitive caudal fin ray : endoskeletal support ratio, approximating 2:1, is found in *Diplocercides, Coelacanthopsis, Lochmocercus,* and variably in *Allenypterus*; all other coelacanths have a derived, 1:1 ratio.

The anatomical information upon which judgements of relationships can be made is scanty for most coelacanths. All coelacanths for which there is adequate information can be separated into two major groups on the basis of characters that mark grades of evolution. All Bear Gulch coelacanths are primitive relative to all others, including the known Devonian forms, in the structure of the cheek. All Hadronectoroidei can be described as primitive relative to all other known coelacanths in having multiple rows of bones in the antorbital region, the relationship of bones to canals in the supratemporal region, the retention of a suboperculum, the structure of the second dorsal and anal fin supports, and, with the exception of *Hadronector,* the pelvic plates. Within the Hadronectoroidei, *Polyosteorhynchus* and *Hadronector* share several characters, such as the notched premaxillae, three extrascapulars, 1:1 caudal fin ray ratio, and rounded first dorsal fin plates, that have been interpreted here as being derived, although all are subject to convergence. *Allenypterus* shares derived states of the lower jaw, shoulder girdle and apparent absence of a basipterygoid process with *Hadronector* and most other coelacanths, is uniquely derived in terms of body form and pelvic association, but is primitive in all other states. *Lochmocercus* seems derived in characters of the supratemporal and supraorbital series and the first dorsal fin plate. There are no clear tendencies within the Hadronectoroidei linking any two species.

The Rhabdodermatidae have an assemblage of primitive cheek characters. They have a uniquely derived perforated premaxilla, highly reduced supratemporal, and a derived pelvic plate, but share derived characters of opercular, supraorbital series bones, and median fin plates with Coelacanthoidei. *Dumfregia huxleyi* could be considered intermediate in known characters between the two major groups.

Diplocercides shares a common derived skull table plan and cheek plan with coelacanthoids, being primitive among all coelacanths in the character of endocranial ossification, basipterygoid process, and caudal fin ray ratio. *Coelacanthus granulatus* is relatively more derived than *Whitea* in cheek reduction, elimination of the antorbital, rostral area reduction, and extrascapular reduction, while being more primitive in posttemporal and supracleithral relationships. *Undina,* which may be an assortment of unrelated forms, has a pelvic plate closely comparable to that of *D. huxleyi* and an apparently primitive number of extrascapulars. *Axelia, Mylacanthus, Scleracanthus, Wimania,* "*Diplurus*" and *Macropoma* share most derived characters in common with *Latimeria.*

The Mesozoic coelacanths, *Coelacanthus granulatus,* and *Latimeria,* with the possible exception of *Undina,* form a tightly interrelated series of species that could be most easily derived from a *Whitea*-like ancestor. *Diplocercides,* despite its geologic isolation, shares its derived characters with the Coelacanthoidei. Early derivation of many of the characters of the coelacanthoids distinguishes them from hadronectoroids even if classification is limited to Paleozoic forms. Although information is lacking on *Euporosteus* and *Coelacanthopsis,* both may provisionally be included within the hadronectoroids. Classification of *D. huxleyi* must await closer study of its cranial osteology.

Characters of the Coelacanthiformes

The unique combination of coelacanth characters can be sumarized as follows—the premaxillae are toothed, do not meet in the midline, and have a low dorsal lamina that may secondarily be emarginated or perforated for pores. There is a small, untoothed median rostral carrying the ethmoid commissure, variably followed by a median postrostral series. Primitively, one postrostral carries the antorbital commissure. Bones of the rostral region may primitively and collectively resemble a mosaic, but all bones are bordered by lateral line canal pores. The roofing bones of the ethmosphenoid moiety of the skull primitively occur in three paired series, the central series overlies the supraorbital canal and the medial series lacks lateral line canal pores, but the central and medial series may fuse. Several anterolateral rostrals, a posterolateral rostral, lacrimojugal, and a postorbital bone carry the infraorbital canal, but the anterolateral rostrals may be reduced in number. The posterolateral rostral always bears a ventral prong associated with the anterior external naris. A central series of bones is primitively found between supraorbital and infraorbital canal bones, primitively associated with the posterolateral commissure, but this series may be reduced or eliminated. The cheek bones primitively consist of tightly fit postorbital, prespiracular, squamosal, quadratojugal, and preoperculum. The quadratojugal bears a vertical pit line, the squamosal the jugal canal, and the preopercular canal traverses the preoperculum and the squamosal but is not continuous with the otic canal dorsally. Secondarily, cheek bones may be reduced to canal tubes or individually lost, and the preopercular canal may come to be borne by the quadratojugal. The quadratojugal is always immediately posterolateral to the high coronoid of the lower jaw. The opercular series primitively consists of a large operculum, a suboperculum, and large lateral gulars; the suboperculum may be secondarily lost. The roofing bones of the oticooccipital moiety of the skull consist of medial postparietals flanked laterally by supratemporals anteriorly and tabulars posteriorly. The supraorbital canal primitively may extend as far posteriorly as the transverse otic pit line, but secondarily does not extend into the postparietal. The otic canal may be carried between postparietal and supratemporal or within the supratemporal but always extends into the tabular. Secondarily, the supratemporal may be reduced or lost. The palate primitively articulates with the ethmoid region anteriorly and to basipterygoid and antotic processes of the ethmosphenoid moieity posteriorly; the basipterygoid process may be secondarily lost. The lower jaw consists of a dentary and infradentary (splenial) anterolaterally, followed by a large angular posteriorly; the mandibular canal being borne by infradentary and angular. Mesially there is a series of coronoids dorsal to the dentary and the large prearticular, the most posterior of which is elevated considerably above the occlusal margin of the jaw and occludes lateral to the posterior end of the ectopterygoid. There are separate retroarticular and articular ossifications in Meckel's cartilage that tend to fuse with growth; the lateral surface of the retroarticular is exposed on the posterolateral corner of the lower jaw, may primitively be ornamented and may primitively possibly bear the posterior end of the mandibular lateral line canal. There are many sclerotics. Postcranially, the wall of the swim bladder is primitively ossified. Neural and haemal arches and spines fuse into median structures. The biserial anal fin is primitively supported proximally by a single element ventral to and braced by the first haemal spines, but secondarily the basal support becomes free in the ventral body wall anterior to the end of the peritoneal cavity. The distal support of the anal fin consists of a series of axial radials. The serial first dorsal fin rays articulate with a single basal plate lying above the neural spines. The biserial second dorsal fin is supported distally by axial elements and proximally by a single dorsal plate, the stem of which is intercalated between neural spines. The second dorsal plate may secondarily bear an articular facet posterodorsally and anterodorsal processes above the neural spines. The caudal fin is internally and externally structurally symmetrical, the serial fin rays being supported by single series of epichordal and hypochordal basal elements, and there is a terminal axial lobe with a terminal tuft of fin rays unsupported by endoskeletal elements. Fin rays are all unbranched, may be primitively ornamented, are not separated by webbing in the first dorsal fin, and primitively occur in 2:1 ratio to endoskeletal supports in the caudal fins. The caudal fin ray : endoskeletal support ratio may secondarily be reduced to 1:1. Scales are cycloid, deeply overlapping, and ornamented by lines or tubercles on the posterior field. External bones of the skull are all ornamented with lines or tubercles that may be secondarily reduced. There is no cosmine, maxilla or submandibular series.

There are several extant schemes of classification that reflect different attempts to relate the coelacanths to the remainder of the Osteichthyes. The modern classical classification incorporates the Coelacanthiformes (Actinistia) and a coordinate group, the Rhipidistia, within the Crossopterygii (Romer, 1966), isolating the coelacanths from the crossopterygians on the one hand, and actinopterygians and dipnoans on the other. A second scheme involves the supergroup Sarcopterygii, which includes dipnoans, choanata (=rhipidistia), and Coelacanthiformes, as a coordinate category distinct from the Actinopterygii (Miles, 1977). Andrews (1973) has treated the Crossopterygii as distinct from Dipnoi and Actinopterygii, indicating that a division into Actinistia and Rhipidistia does not reflect the continuous nature of character transformations now known, and has suggested the terms Quadrostia and Binostia to include Osteolepiformes, Rhizodontiformes, and Onychodontiformes as opposed to Porolepiformes and Coelacanthiformes. New information from the Bear Gulch coelacanths has established that the skull table did indeed evolve separately in Porolepiformes and Coelacanthiformes, both possibly from the type X skull table of Andrews (1973). The type X skull table is also primitive for Actinopterygii, except that the extratemporal is presently unknown in either coelacanths or actinopterygians.

The Bear Gulch coelacanths make it possible to refine conceptions of the primitive states and character transformations within the order, and this information and new information on the Paleozoic Actinopterygii provide an opportunity to reexamine the interrelationships of the Osteichthyes.

OSTEICHTHYAN INTERRELATIONSHIPS

Several critical assumptions must be made in any judgement of interrelationships, especially one in which the evidence is as scanty and as subject to differing interpretations as is the case here. The first and most sweeping is that there is no derived relationship between Dipnoi and Holocephali, as discussed in part by Miles (1977; see Lund, 1977). Also assumed, and discussed above, are that the absences of a maxilla, a submandibular series, and branchiostegal rays are secondary characters, whereas the absence of choanae among the osteichthyans is a primitive feature; further, that the intracranial joint arose but once and was secondarily modified in Coelacanthiformes. It is also assumed, by reference to the Chondrichthyes (Lund, in press) that a baseost-axonost supporting skeleton for the median fins, including the caudal fin, is primitive. Neither the chondrichthyan nor acanthodian conditions, however, are relevant to the present discussion. It is unfortunate, furthermore, that the term "mosaic of snout bones" has to be used, for it carries very little information aside from the observation that there were many, relatively unintelligible, tightly fitting elements.

Comparison of actinopterygians to other Osteichthyes reveals that all other osteichthyans (Sarcopterygii) are derived relative to cheek bone reduction, completeness of the preopercular canal, completeness of the prespiracular series of bones, condition of the opercular-branchiostegal series, and the state of fusion of the neural elements of the axial skeleton (Table 8). Actinopterygians share no derived characters in common with dipnoans. They do share the skull table pattern at the posterior end of the braincase with all "crossopterygians" and the reduction in numbers of longitudinal skull bone series to two with the "rhipidistians." The skull table pattern has demonstrably been arrived at in parallel within Dipnoi, and skull roof patterns during the evolution of the actinopterygians has converged upon or approximated even the porolepoid pattern, leading to the caution that this character is subject to convergence. The reduction of numbers of longitudinal series can be demonstrated to occur within dipnoans as well as within coelacanths, and is therefore also relatively unreliable. The assumptions based upon caudal structure and symmetry, however, suggest the independent evolution of the heterocercal caudal fin among several groups. This set of assumptions can only be tested by further study of the internal structure of the skeletons. The Actinopterygii are therefore considered the primitive collateral group of all other Osteichthyes, a grouping to which the term Sarcopterygii has been applied (Romer, 1966) (Fig. 77).

The dipnoans are primitive in the multiple series of endoskeletal supports for the caudal fin, a character that needs more data. They share primitively with Actinopterygii the greater posterior extent of the supraorbital canal, the absence of an intracranial joint, and the supraneural-baseost-axonost character of dorsal and anal fin supports (Table 8). They share with all Crossopterygii the derived conditions of the cheek bones, where they are closest to the Porolepiformes primitively, the course of the lateral line canals of the cheek, the specializations of median and lateral gulars, the fused neural arches and spines, similar reductions of the prespiracular series of bones (although they represent an extreme among this group), and the presence of cosmine. Other characters not given in Table 8 but possibly pertinent here are the common possession of two dorsal fins in contrast to the single dorsal of primitive Actinopterygii, and the mutual tendency among porolepoids, osteolepoids and dipnoans to fuse the rostral area into a solid unit. The dipnoans share with coelacanths only the absence of a maxilla and reduction of the branchiostegal series. The dipnoans seem to share sufficient derived characters with all other osteichthyan groups but the actinopterygians to justify the term Sarcopterygii.

The coelacanths are primitive among Crossopterygii, and the remainder of the crossopterygians derived, in the presence of an antorbital commissure, the number of bone series in the anterior part of the skull roof, the separation of the premaxillae

Table 8.—*Comparisons of character states among the Osteichthyan groups. Abbreviations: Actin., Actinopterygii; Coel., coelacanthiformes; Onych., Onychodontiformes; Osteol., Osteolepiformes; Poro., Porolepiformes; P, primitive;* D^{1-n}*, derived character states one through n, usually implying a continuum;* D^9*, separately derived state. See text for discussion of characters.*

Character	Actin.	Dipnoi	Coel.	Onych.	Poro.	Osteol.
Supraorbital canal to skull rear	P	P	D^1	D^1	D^1	D
Antorbital commissure	D	P	P	D	D	D
3 longitudinal bone series	D	P	P	D	D	D
2 series posterior to orbit	D^1	P	D^1	D^1	D^2	D^1
Rostral between premaxilla	P	—	P	D	D	D
Anterolateral rostrals	P	—	P	P	D	D
"Mosaic" snout bones	D	P	P	P	P	D
Premaxilla	P	—	P	—	D^9	D^9
Cheek bones (many-few)	P	D^1	D^3	D^2	D^1	D^3
Complete preopercular canal	P	D	D	D	D	D
Preopercular canal bones	D?	P	D^1	D	D	D^1
Prespiracular series	P	D^9	D	D	D	D^1
Infradentaries	D^9	P	D^1	D	D	D
Maxilla	P	D	D	P	P	P
Branchiostegal series	P	D^1	D^2	D	D	D
Submandibular series	D	P	D	P	P	P
Intracranial joint	P	P	D^2	P	D^1	D^1
Choanae, internal	P	P	P	P	D	D
Interclavicles	D	P	D	P	P	P
Anal fin support, proximal	P	P	D	—	D	D
Anal fin support, distal	P	P	D	—	D^2	D
Neural arch-spine	P	D	D	—	D	D
First dorsal support, proximal	P	P	D	—	D	D
First dorsal support, distal	P	P	D^2		D^1	D^1
Second dorsal support, proximal	—	P	D^2	?	D^9	D^1
Second dorsal support, distal	—	P	D^2	?	D^1	D^1
Caudal fin symmetry	D	P	P	P	D	D
Cosmine	P	D	?	D	D	D

by the rostral and lack of a lateral line canal, and the absence of cosmine. Alternatively, however, the coelacanths show potential derivation from a sarcopterygian state in the presence of lateral gulars and absence of a median gular and branchiostegals, from all rhipidistians in the loss of a maxilla with retention of the basic character of the neighboring bones, and in the presence of at least one infradentary. The coelacanths also share with osteolepoids, very similar preopercular canal bones and quadratojugal, characters that could be derived through reduction either from porolepoid or onychodontoid states. They share with all known Crossopterygii the unique dorsal and anal fin supports, although they are further derived in the condition of the first dorsal support. They can be counted as primitive among Crossopterygii in the structural symmetry of caudal fin endoskeleton, possibly sharing this position with the Onychodontiformes.

The osteolepiform and porolepiform fish, called choanates, share derived conditions of the anterolateral rostral area and anterior infraorbital canal, the position of the premaxillae and rostral, the presence of choanae, and the structure and symmetry of the caudal fin.

There are, therefore, several alternative schemes of interrelationships of the Osteichthyes under the above assumptions, depending upon the emphasis placed upon character derivations that are almost all losses or reductions. The actinopterygians are less closely related to other osteichthyans than they are to each other, leading to the suggestion of a primary binary division into Actinopterygii and Sarcopterygii. Within the Sarcopterygii, if one chooses to emphasize the significance of the relationship between choanates, as seems to us to be the most parsimonious choice based upon the least number of possible parallelisms, a scheme as in Fig. 77B suggests itself. If, however, it is assumed that among other elements the coelacanths have lost are the internal choanae and a flexible air bladder, there are several derived resemblances between Coelacanthiformes and Osteolepiformes that can be emphasized, as in Fig. 77A. Either scheme fails adequately to take into consideration that the coelacanths are unique among a spectrum of related groups. The terms rhipidistia and actinistia in particular imply separate derivation of the two from a common stock, an idea that can no longer be justified.

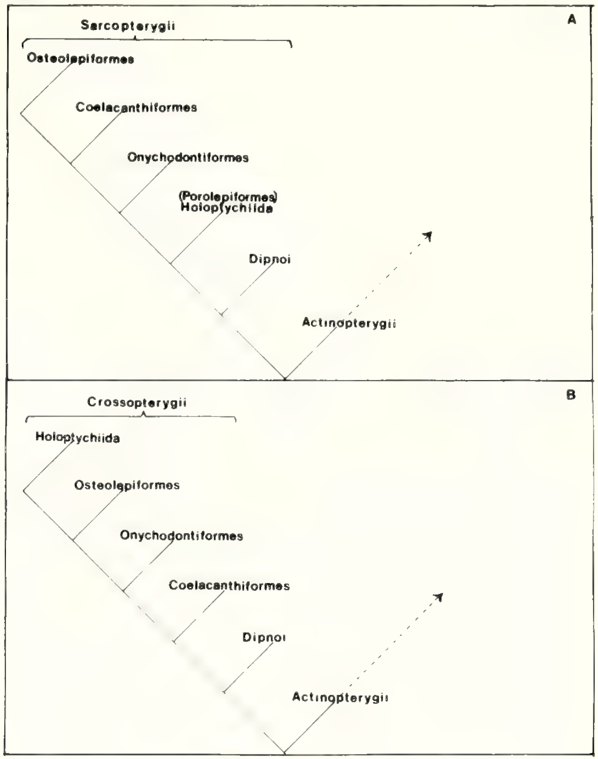

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Fig. 77.—Alternative schemes of Osteichthyan interrelationships. See text for explanation.

CLASSIFICATION

The broad systematic conclusions of this paper can be summarized in an outline classification.

- Class Osteichthyes
  - Subclass Actinopterygii
  - Subclass Sarcopterygii
    - Infraclass Dipnoi
    - Infraclass Crossopterygii
      - Superorder Achoana
        - Order Onychodontiformes
        - Order Coelacanthiformes
          - Suborder Hadronectoroidei
            - Family Hadronectoridae
          - Suborder Coelacanthoidei
            - Family Diplocercidae
            - Family Rhabdodermatidae
            - Family Coelacanthidae
            - Family Laugiidae
      - Superorder Choanata
        - Order Osteolepiformes
        - Order Rhizodontiformes
        - Order Porolepiformes

FUNCTIONAL RELATIONSHIPS

Point by point analysis of characters, with the aim of understanding interrelationships of groups, negates, obscures, or ignores the functional integration of the characters that in their totality render the groups separate biological entities with unique adaptive pathways. The Coelacanthiformes incorporate a large number of cranial characters into a feeding mechanism quite distinctive in function from the groups of fish with which it can be related as well as from any other group of Paleozoic fish. The postcranial characters are also summed up in a particular propulsive mechanism with distinctive characteristics relative to the other members of Paleozoic ichthyofaunas. Without detailed exposition of the functions of the basal osteichthyan groups, a short summary of contrasting conditions may be helpful to an understanding of the coelacanth adaptive pathway.

The basic feeding mechanism of all coelacanths involves suction, rather than delivery of power to the bite as in other Crossopterygii and primitive Actinopterygii (Lund et al., in press). The leverage arrangements of the palate-braincase articulation produced by the antotic process (Thomson, 1970) of coelacanths decouples the jaw and anterior moiety of the braincase, compared to the arrangement of the crossopterygian feeding mechanism. Restriction of the gape by a high coronoid, rather than by shortening the jaw as in teleosts, produces not more power delivered to a bite that lacks teeth in almost all coelacanths, but a nozzle with intake diameter restricted and consequent adjustment of intake velocity. The evolution of fleshy lips with maintenance of a long lower jaw may be seen to serve several functions, channeling and restriction of water flow in respect to the aperture and to timing of opening of the mouth, and restriction of the direction of water flow in the event of large mouth opening. The absence of strong biting forces delivered to the anterior part of the braincase can be related in turn to several different developments within coelacanths, such as the lack of consolidation of external bones into a solid unit or tightly knit mosaic to brace against the lower jaw, the absence of a maxilla, the reduction of the dentary, and reduction of ossification in the ethmosphenoid moiety of the braincase. Reduction of the opercular series and decoupling of the gulars from the operculum, backward extension of the soft opercular flap, freeing of the shoulder girdle from the braincase dorsally and an increasingly mobile interrelationship of shoulder girdle elements, the development of cervical vertebrae, and repeated tendencies to articulate the operculum (hyoid and operculum?) directly with the posteriormost corner of the braincase, can all be correlated with intracranial involvement in the operation of the opercular-branchial pump, as distinct from the palatal suction pump (Lund et al., in press). Thus, while the coelacanths share with other crossopterygians an intracranial joint that undoubtedly indicates a close morphogenetic and phylogenetic relationship, they have diverged from the ancestral stock along a quite unique adaptive line in terms of feeding mechanism. They are far removed indeed from either the autostylic, well braced dipnoans or the actinopterygian adaptation for speedy closure of the mouth with a firm bite.

The coelacanth postcranial skeleton, consisting of lobed paired and median fins (except the first dorsal fin) and a broadly expanded caudal fin with individual endoskeletal supports for both epichordal and hypochordal components, corresponds closely to that of other crossopterygians as well as to dipnoans. These fish can all be broadly characterized as having high drag bodies with tails of low aspect ratio, indicative of potentially high acceleration but low sustainable cruising speed (Dicanzio, in press). The mobility and positions of the median and paired fins would confer high ability to maneuver, as would characterize lurking predators or slow cruising feeders (Andrews and Westoll, 1970*a*; Keast and Webb, 1966). In this regard, the coelacanths differ the least from the Onychodontiformes, the crossopterygian group most distinct from them in feeding adaptations. The actinopterygian body form contrasts sharply with that of all sarcopterygians in having a relatively low drag profile and in having higher caudal aspect ratios; the former condition resulting from the single dorsal fin, the lack of fleshy extensions and the generally compressed body and the latter condition made possible by the heterocercal tail. Lurking predators among the actinopterygians tend to have rounded caudal outlines, rounder body cross sections and even in the Bear Gulch, lobed pectoral fins (Keast and Webb, 1966; Dicanzio, in press; Lowney, 1980; Andrews and Westoll, 1970*a*).

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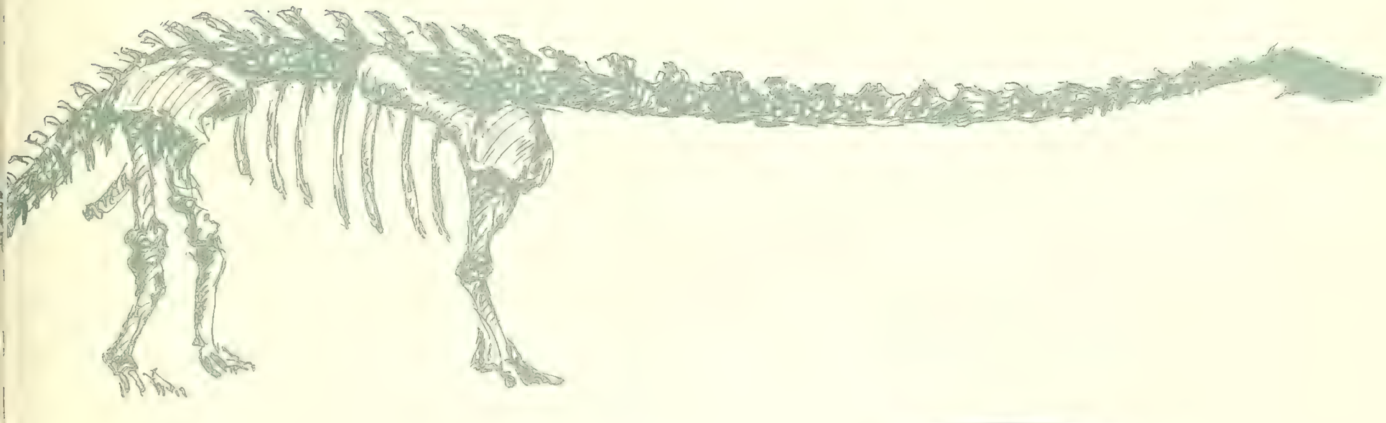

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ARIKAREEAN, HEMINGFORDIAN, AND BARSTOVIAN MAMMALS FROM THE MIOCENE COLTER FORMATION, JACKSON HOLE, TETON COUNTY, WYOMING

ANTHONY D. BARNOSKY

NUMBER 26

PITTSBURGH, 1986

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ANTHONY D. BARNOSKY

Assistant Curator, Section of Vertebrate Fossils

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ABSTRACT

Miocene mammal faunas of three different land-mammal ages are superposed in the Colter Formation of Jackson Hole, Wyoming. The late-early Arikareean (=ca. 23–25 mya) Emerald Lake Fauna most closely resembles those of the upper half of the *Meniscomys* Concurrent-range Zone and includes the new aplodontid *Allomys cristabrevis,* new species, and the new leporid *Archaeolagus emeraldensis,* new species. The East Pilgrim Assemblage is composed of fossils from at least two, and maybe three, stratigraphically separate localities. The stratigraphically highest local fauna in the Assemblage is one of the few of early Hemingfordian age (ca. 18–19 mya) known from the Montana–Wyoming Rockies. It shares species with faunas of the Runningwater Formation in Nebraska. However, the stratigraphically lowest oreodont in the East Pilgrim Assemblage is referred to *Merychyus arenarum,* a species that is common in the late Arikareean Marsland Formation (=Hunt's, 1985, Upper Harrison beds). Both the Emerald Lake Fauna and the East Pilgrim Assemblage are found in andesitic, trachytic, and latitic tuffaceous rocks probably indicative of compressional-type volcanism and tectonism. The Cunningham Hill Fauna, containing the first late Barstovian (=ca. 12–14 mya) small mammals described from Wyoming, correlates with the *Copemys longidens* or *Copemys russelli* Assemblage Zones of the Barstow Formation; it includes the new species *Oreolagus colteri,* new species (ochotonid), *Lignimus transversus,* new species, and *Mojavemys magnumarcus,* new species (geomyids). The Cunningham Hill Fauna also yields the first northern Rocky Mountain records for *Petauristodon, Diprionomys agrarius, Lignimus, Mojavemys, Copemys kelloggae,* and *Schaubeumys.* The Cunningham Hill Fauna occurs in rhyolitic tuffaceous rocks usually associated with extensional volcano-tectonic regimes. All of the Colter faunas show greater affinity with Great Plains faunas than with those west of the Rockies. The Arikareean and Barstovian faunas are composed of suites of species that differ from similarly aged assemblages of the Great Plains and Far West, apparently because ecological conditions were different. The suite of species in the Cunningham Hill Fauna provides evidence that the terms "early Valentinian" and "late Barstovian" refer to overlapping intervals of geologic time.

INTRODUCTION

Fossil mammals from the Colter Formation of Jackson Hole, northwestern Wyoming, occur in an intermontane basin of both geological and paleontological interest. The geological interest stems from the remarkably thick Tertiary section—some 12 km with rocks of every epoch—of which the Colter comprises a significant part (1,500 m). Such thick deposits are uncommon in intermontane basins of the northern Rocky Mountains, and record a complex history of Tertiary volcanism and tectonism in Jackson Hole (Barnosky, 1983, 1984; Behrendt et al., 1968; Love et al., 1973, 1978; and references therein). The fossil mammals are important in dating the tectonic events and in providing a geographic link between well known faunas of the Far West (=Oregon, California, Nevada) and the Great Plains. This report analyzes three distinct faunas of Miocene mammals from the Colter Formation, describes five new species, dates a probable change from compressional to extensional-type volcanism in northwestern Wyoming, and discusses interregional relationships between faunas of the northern Rocky Mountains, the Far West, and the Great Plains. The geology of the Colter Formation in particular and Jackson Hole in general is reported separately (Barnosky, 1983, 1984; Love and Reed, 1971; Love et al., 1973).

The youngest fauna, of late Barstovian age, is the most diverse and is the first record for small mammals of this age in Wyoming. Only two other Barstovian occurrences of small mammals have been published for the northern Rockies, the Anceney fauna of Gallatin County (Dorr, 1956) and the Flint Creek fauna of Granite County, Montana (Black, 1961). Both of the published faunas are small, although Sutton (1977) in an unpublished doctoral dissertation showed a greater diversity at Anceney. The Hemingfordian and Arikareean faunas from Jackson Hole, while sparsely represented, provide the only Rocky Mountain records for some taxa.

LIST OF ABBREVIATIONS

AMNH—American Museum of Natural History. AUG—Augustana College. CMNH—Carnegie Museum of Natural History. F:AM—Frick Collection, American Museum of Natural History. FMNH—Chicago Field Museum of Natural History. LACM—Los Angeles County Museum of Natural History. KUVP—University of Kansas Museum of Natural History. ROM—Royal Ontario Museum. SDSM—South Dakota School of Mines and Technology, Museum of Geology. UCMP—University of California Museum of Paleontology. UMMP—University of Michigan Museum of Paleontology. UNSM—University of Nebraska

State Museum. UO—University of Oregon Museum of Natural History. USGS—United States Geological Survey. USNM—Smithsonian Institution, United States National Museum. UWBM—Thomas Burke Memorial Washington State Museum, University of Washington. UWYO—University of Wyoming Museum of Geology. YPM—Yale Peabody Museum. AP—longest anteroposterior diameter. T—widest transverse diameter. TA—widest transverse diameter, anterior half of tooth. TP—widest transverse diameter, posterior half of tooth. my(a)—million years (ago).

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GEOLOGIC SUMMARY OF COLTER FORMATION

The Colter Formation, a complexly bedded sequence of volcaniclastics, is confined to Teton County, Wyoming, and mostly to Jackson Hole (Figs. 1 to 3). All exposures crop out along streams and slide scarps and most are within or adjacent to Grand Teton National Park. Measured sections summarized in Figs. 4 to 8 and described in detail by Barnosky (1983, 1984) show that at least 70 distinct beds are superposed to form the Colter and can be broadly grouped into two very distinctive members.

The Crater Tuff-breccia Member composes the bottom third of the formation, Units 1 through 34, and is characterized by interbedded tuffs and tuff-breccias of andesitic, trachytic, and latitic composition. It is confined to the area around Pilgrim Creek, Two Ocean Lake, and Emerald Lake. Distinctive features in outcrop include (1) gray to very bright green color and (2) abundant angular tuff-breccias that seldom include quartz cobbles. Chemically, the rocks can be distinguished by a relatively low SiO2 content (less than 72% recalculated water-free). In contrast, the overlying Pilgrim Conglomerate Member, Units 35 through 70, is composed of conglomerate, sandstone, and claystone, as well as tuff and tuff-breccia. The member is rhyolitic and further differentiated from rocks in the lower member by (1) pink, tan, green, blue-gray, or white color and (2) frequent occurrence of rounded quartzite cobbles within conglomerates that are made mostly of angular to sub-rounded volcanic rocks. Chemically, SiO2 contents above 72% characterize tuffs in the Pilgrim Conglomerate Member, which crops out near Pilgrim Creek, Two Ocean Lake, Cunningham Hill, Shadow Mountain, and Ditch Creek. The mid-Tertiary unconformity (Fields et al., 1985; Rasmussen, 1973; Thompson et al., 1982; and references therein) apparently coincides with the abrupt contact between the two members, and may be represented by the unconformable contact of the upper member with Paleocene rocks on Shadow Mountain. Faults (Fig. 2) cause repetition of Units 2 through 19 along East Pilgrim Creek (Fig. 4), and of most of the Pilgrim Creek section (Figs. 4, 5) along Two Ocean Lake (Fig. 7).

Near-vent facies of ignimbrite and coarse tephra show that both members accumulated on and near the flanks of volcanoes that were active in northwestern Jackson Hole through much of the early

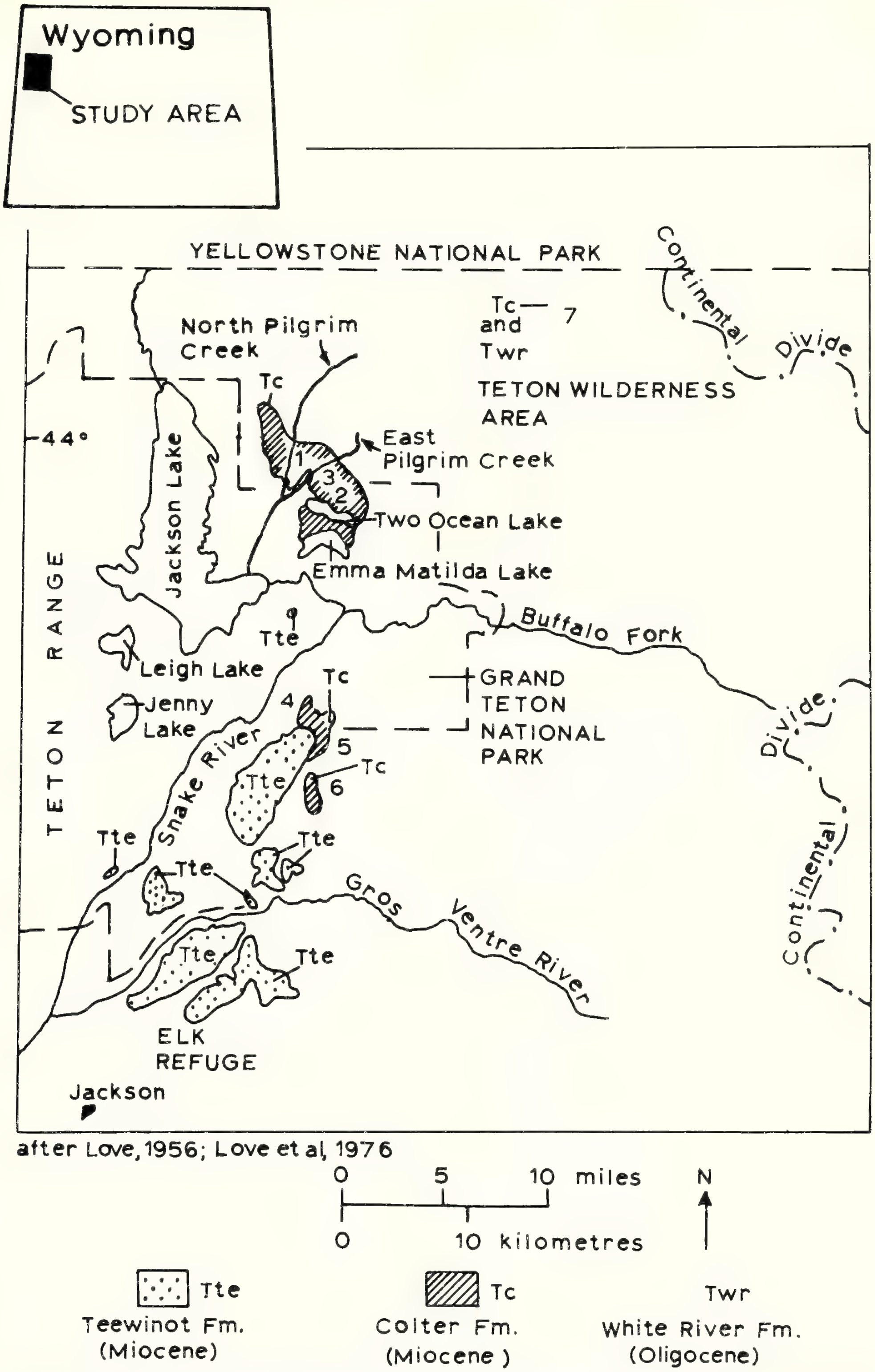


Fig. 1.—Geographic index map. Numbers show geographic areas mentioned in text. 1—Pilgrim Creek, 2—Two Ocean Lake, 3—Crater Mountain, 4—Cunningham Hill, 5—Shadow Mountain, 6—Ditch Creek, 7—Emerald Lake.

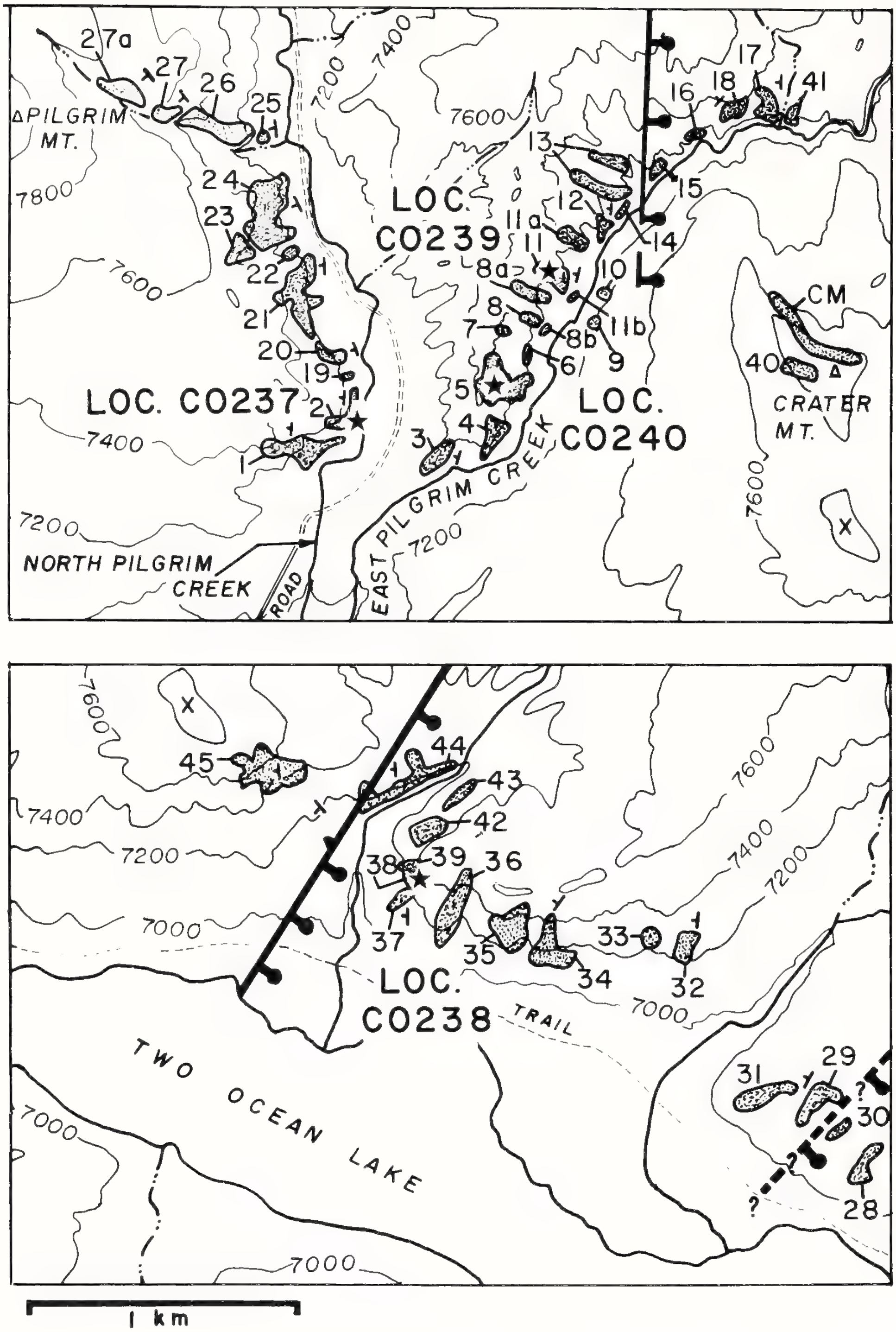


Fig. 2.—Detail maps. *Top:* Region around Pilgrim Creek (Area 1 in Fig. 1) and Crater Mountain (Area 3). *Bottom:* Region around Two Ocean Lake (Area 2). Numbers identify stippled outcrops that were prospected and through which sections were measured. Topographic base is redrafted from part of Two Ocean Lake 7.5′ Quad. X's show where upper and lower maps overlap. Stars indicate UWBM fossil vertebrate localities. Heavy black lines show major faults; dots on short bars mark downthrown block. Contour interval 200 ft. North at top.

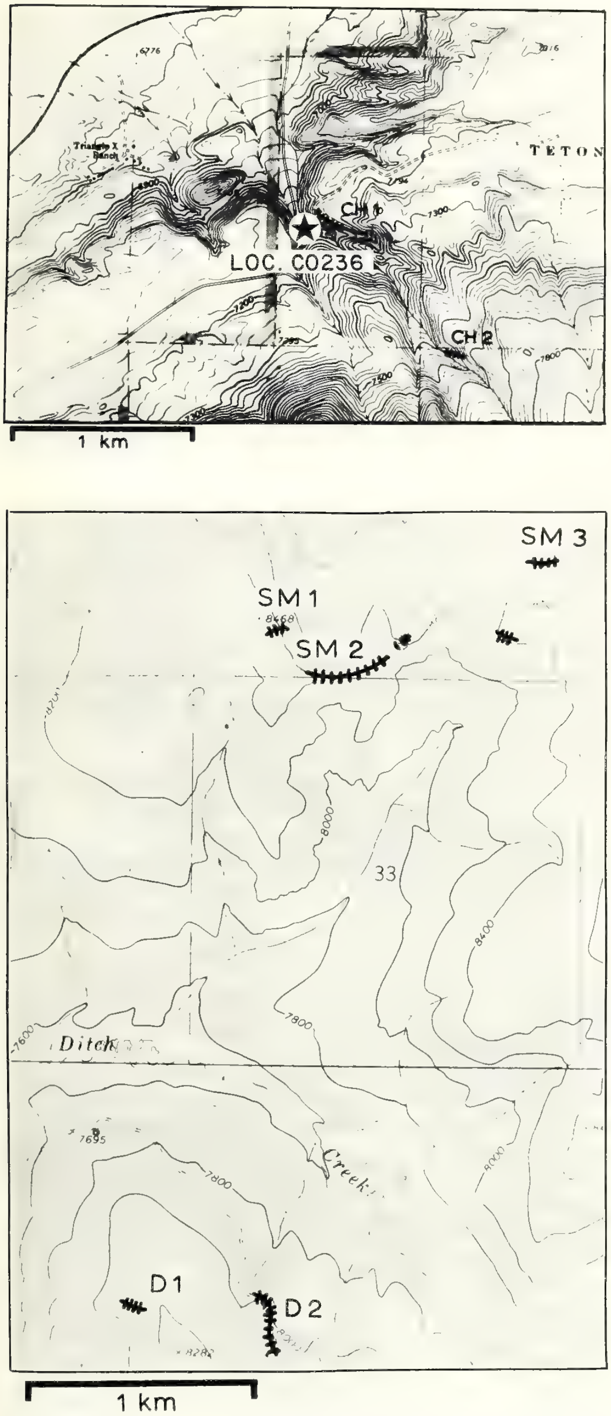


Fig. 3.—Detail maps. *Top:* Cunningham Hill (Area 4 on Fig. 1). Base is part of Moran 7.5′ Quad. *Bottom:* Shadow Mountain (SM) and Ditch Creek (D) (Areas 5 and 6). Base is part of Shadow Mountain 7.5′ Quad. Heavy lines with cross bars identify outcrops that were prospected and through which sections were measured. Stars indicate UWBM fossil vertebrate localities. Contour interval 40 ft. North at top.

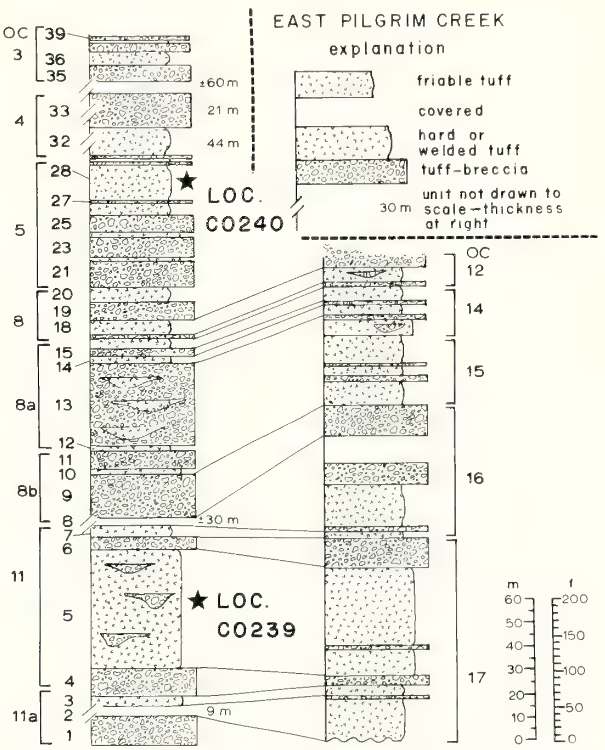


Fig. 4.—Lower third of the type section of the Colter Formation, measured along East Pilgrim Creek (Area 1 on Fig. 1). Numbers to the left of the section identify lithologic units. Brackets denote outcrops (OC) through which units were measured. Numbers outside the brackets label outcrops, which correspond to those shown on Fig. 2. Stars indicate UWBM fossil vertebrate localities.

and middle Miocene (Barnosky, 1983, 1984). The Colter Formation thus represents the only volcanic center known to be active in northwest Wyoming-southwest Montana between 20 and 8 my ago (Chadwick, 1981). The andesitic, trachytic, and latitic tuffs in the lower member suggest that volcanism was associated with compressive tectonics, whereas rhyolitic tuffs in the upper member are characteristic of volcanic activity in an extensional regime (Lipman et al., 1972; Christiansen and Lipman, 1972). The formation therefore apparently records the Mid-Tertiary change from compressional to extensional tectonics that took place throughout the western U.S. (Stewart, 1978; Christiansen and Lipman, 1972; Lipman et al., 1972), and provides an opportunity for more precisely dating the change in the Montana-Wyoming region. At present, fossil mammals give the only reliable dates for the Colter Formation. Problems with excess argon in glass shards and allogenic sanidine crystals have complicated attempts at K-Ar age determinations.

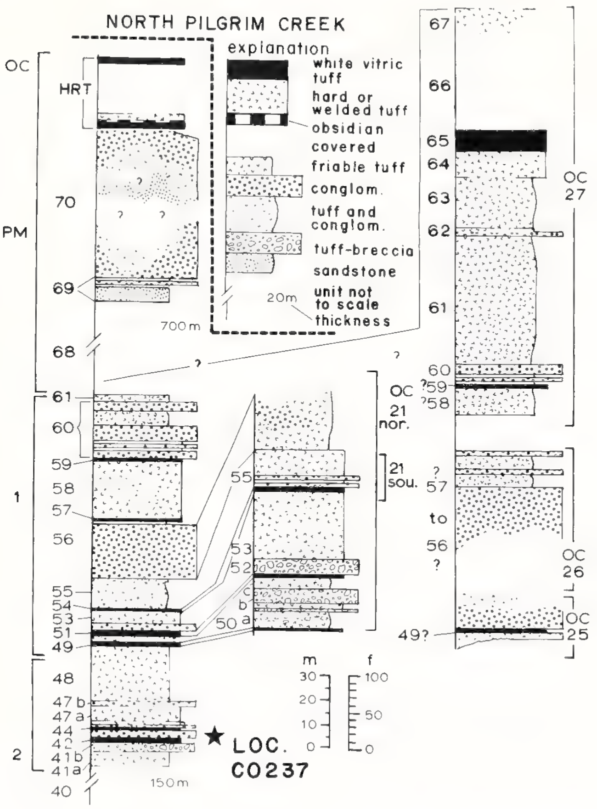


Fig. 5.—Upper two thirds of type section of the Colter Formation, measured along North Pilgrim Creek (Area 1 on Fig. 1). Star indicates UWBM fossil vertebrate locality. See Fig. 4 for further explanation.

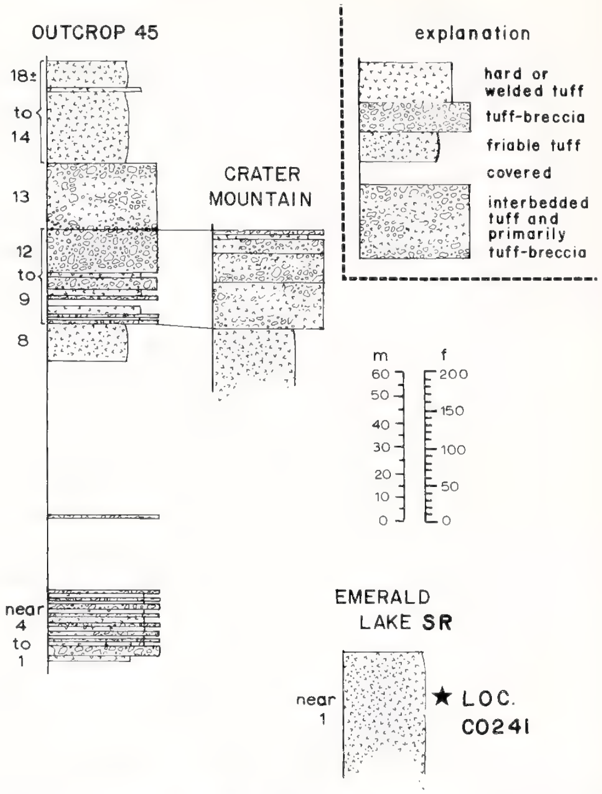


Fig. 6.—Stratigraphic sections at Outcrop 45 (Area 2 on Fig. 1), Crater Mountain (Area 3), and Emerald Lake (Area 7). Unit numbers correspond to those in Fig. 4, where further explanation is given. Star indicates UWBM fossil vertebrate locality.

HISTORY OF PALEONTOLOGICAL INVESTIGATIONS

In the late 1930's a local cowboy, Roy Saunders, reported the first vertebrate fossils from Jackson Hole. The bones were *in situ* along East Pilgrim Creek somewhere between Units 5 and 28, and included the skull of an oreodont (*Merychyus*) and foot bones of the camel *?Oxydactylus* (Colbert, 1943; Schultz and Falkenbach, 1947). Subsequently, J. D. Love began detailed geologic investigations in the area and found the East Pilgrim 5 (UWBM loc. C0240) and Cunningham Hill (UWBM loc. C0236) localities. By the late 1960's, his continued efforts along with those of C. C. Black, M. R. Dawson, and M. C. McKenna had produced small faunas from Cunningham Hill (UWBM loc. CO236), Emerald Lake (UWBM loc. C0241), and East Pilgrim 5 (UWBM loc. C0240). In 1968, enough material existed for Black to suggest a Hemingfordian age for the East Pilgrim 5 and Cunningham Hill assemblages, which agreed with earlier interpretations by Love (1956). With continued collecting by J. F. Sutton, it became apparent that strata at Cunningham Hill were somewhat younger, perhaps Barstovian in age (Sutton and Black, 1972). Sutton and Black also concluded that the East Pilgrim 5 assemblage resembled faunas of the Runningwater Formation (late-early Hemingfordian). Later, Love et al. (1976) determined the age of the Emerald Lake locality to nearly equate with that of the Monroe Creek Formation (late-early Arikareean), and Sutton and Black (1975) described Chadronian mammals from below the Colter Formation (OC 41 of Fig. 2). Most of the reports on Colter fossils were based on fragmentary specimens that commonly were few in number. Therefore in 1978, at the suggestion of Love, work culminating in this report began in order to more precisely determine the taxonomic, biostratigraphic, and biogeographic affinities of the mammals from the Colter Formation.

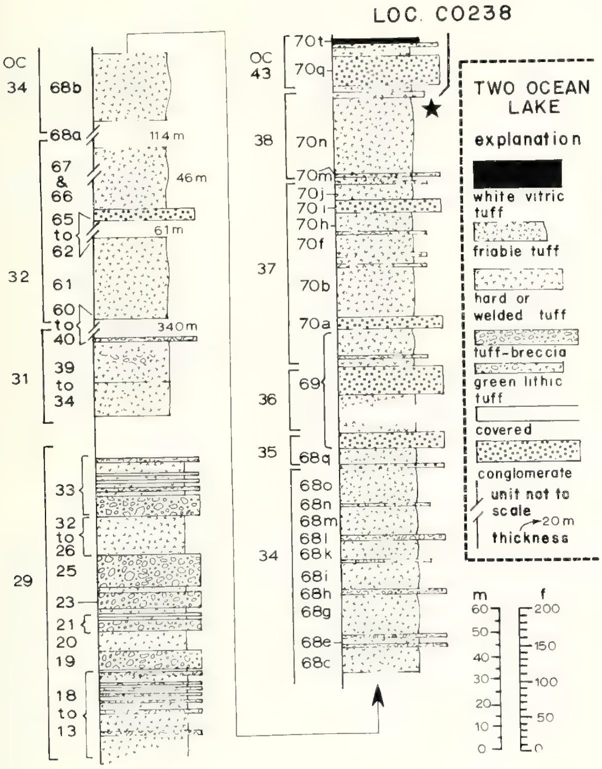


Fig. 7.—Stratigraphic section along north shore of Two Ocean Lake (Area 2 on Fig. 1). Unit numbers correspond to those in Figs. 4 and 5, where further explanation is given. Star indicates UWBM fossil vertebrate locality.

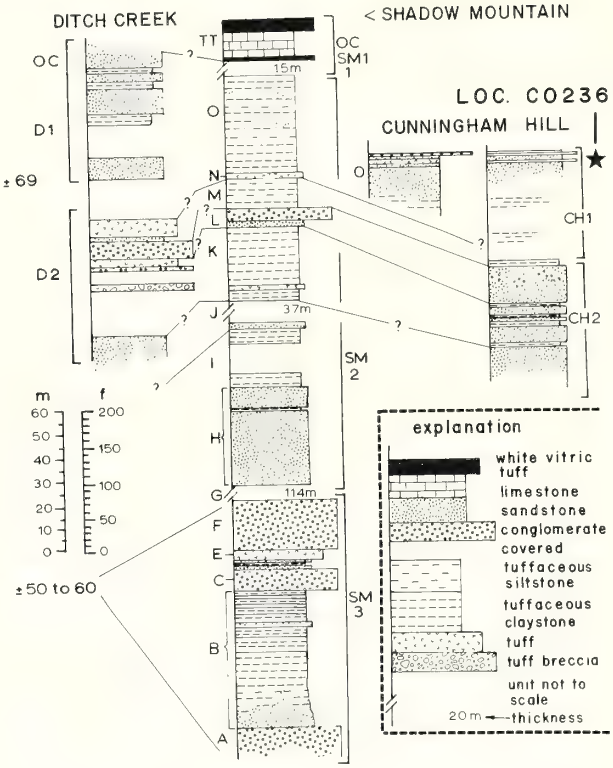


Fig. 8.—Stratigraphic section through Ditch Creek (Area 6 on Fig. 1), Shadow Mountain (Area 5), and Cunningham Hill (Area 4). Outcrops through which the sections were measured are mapped on Fig. 3. Capital letters designate units where lenticularity of beds, geographic separation, and different facies prevent direct correlation to type section; ± numbers at left indicate approximate match to type section. Star indicates UWBM fossil vertebrate locality.

METHODS

FIELD

Outcrops of the Colter Formation within the heavily-vegetated study area were located from air photos, 7.5′ orthophotos, and 7.5′ geologic maps (Love, 1973 and unpublished data) corresponding to the Two Ocean Lake, 1968, Moran, 1968, Shadow Mountain, 1968, and Mount Hancock, 1959, USGS topographic map quadrangles. Each outcrop mapped on Figs. 2, 3, and in Love et al. (1976:fig. 3) was systematically searched at approximately 2-m contour intervals to locate flakes of fossil bone at least 2 mm in size. Where bone occurred, enough matrix to fill at least one burlap feed bag (about 100 lbs or 45 kilos) was washed through screens containing 16 squares per 1 inch (about 12 squares per 1 cm). Resulting concentrate was dried and searched in the field without magnification and was deemed rich enough for additional collecting with recovery of one or more identifiable cheek teeth per 45 kilos of unwashed matrix. The only two sites rich enough were North Pilgrim 2 (UWBM loc. C0237) and Cunningham Hill (UWBM loc. C0236), from which totals of 2,585 kilos (about 5,700 lbs) and 3,120 kilos (6,875 lbs) of matrix, respectively, were washed. After drying in the field, concentrate was sorted into size fractions by shaking it through a series of five nested, spring-mounted screens with mesh sizes of 4, 8, 16, 20, and 30 squares per inch. The 4 and 8 mesh fractions were searched and discarded in the field. Concentrate finer than 30 mesh was not searched. Large bones were collected by standard plaster bandaging techniques when necessary.

To place fossils within the proper stratigraphic context, detailed sections were measured through each outcrop and could usually be correlated with the continuous type section along Pilgrim Creek by marker beds, lithologic similarities, or superpositional relationships. For each of the sections, each lithologically distinct stratum was considered a Unit for which thickness to the nearest decimeter, rock type, grain size, roundness, sphericity, cementation, composition, color, sorting, bedding, sedimentary structures, fossils, orientation of paleocurrent indicators, and strike and dip were determined. Faults were recognized by detailed repetition of units in association with slickensides and extremely fractured rock.

LABORATORY

The 16 mesh concentrate was generally searched under a 1.5× illuminated magnifier and smaller size fractions under an 8×

binocular microscope. Ninety-two identifiable teeth were recovered from the Cunningham Hill concentrate, and 162 from North Pilgrim 2. Measurements smaller than 5 mm were taken through a grid-reticule mounted on the ocular of a Nikon binocular microscope at 31×. Dial calipers were used for measurements between 5 mm and 140 mm, and a mm rule for those over 140 mm. Unless otherwise noted, all anteroposterior and transverse measurements of teeth are maxima (not necessarily at the occlusal surface) and the transverse measurement was taken perpendicular to the anteroposterior one. For geomyoid teeth, maxima in occlusal view did not differ significantly from maxima taken in side and posterior views.

All published specimens were examined except for Saunders' material, which is well illustrated in Colbert (1943) and Schultz and Falkenbach (1947). In the systematics, the use of "cf." denotes tentative referral to a species. The use of "near" denotes a species that cannot be definitely determined with the material at hand, is morphologically most similar to a given form, but shows some characters suggestive of a new species. When the material warrants only generic identity, the name of the genus is followed by "species indeterminate."

Radiometric dates have been corrected by the IUGS constants listed in Dalrymple (1979) unless noted otherwise.

FOSSIL OCCURRENCES

Although fossil mammals are generally scarce in the Colter Formation, they fortuitously occur near the bottom and top of each member (Table 1). In the lower member unit 1SR (UWBM loc. C0241), Unit 5 (UWBM loc. C0239), and Unit 28 (UWBM loc. C0240) have yielded fossils. Unit 1SR (Fig. 6) lies at the base and Unit 28 (Fig. 4) is near the top of the member; these two units approximately bracket the part of the Colter formed by compressional-type volcanism. The upper member produced fossils from Unit 43 (UWBM loc. C0237), Unit O (UWBM loc. C0236), and Unit 70o (UWBM loc. C0238). The assemblage from Unit 43 (Fig. 5) is near the base of the upper member and provides a minimum age for the inception of extensional-type volcanism. The Unit O assemblage (Fig. 8) probably occurs in the upper third of the upper member.

Fossils are superposed in the type section along East and North Pilgrim Creeks. The fossiliferous Unit 1SR, although cropping out some 30 km to the northeast near Emerald Lake (Fig. 1, Area 7), correlates with beds near Unit 1 in the type section on the basis of lithologic similarities. Tuff of both areas is massive, gray, fine grained, vitric, and friable to moderately indurated in most exposures. Unit O at Cunningham Hill apparently correlates with strata near Unit 69 in the type and Two Ocean Lake sections, because only in these areas are bluish rocks, yellow-green sandstones with pumice chunks, laminated whitish-tan tuff, and tan conglomerate found interbedded. Localities that have yielded only one taxon each occur in Unit 5 of the East Pilgrim section (Fig. 4) and Unit 70o of the Two Ocean Lake section (Fig. 7). Precise geographic positions of the fossil localities are as follows.

Cunningham Hill, UWBM loc. C0236.—43°45.7′N, 110°33.31′W, NE ¼ of SE ¼ Sec. 20, T. 44 N, R. 114 W, Teton County, Wyoming, Moran 7.5′ Quad, 1968. In Unit O, Pilgrim Conglomerate Member of Colter Formation.

North Pilgrim 2, UWBM loc. C0237.—43°55.81′N, 110°33.63′W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5′ Quad, 1968. In Unit 43, Pilgrim Conglomerate Member of Colter Formation.

Two Ocean Lake, UWBM loc. C0238.—43°55.25′N, 110°31.57′W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5′ Quad, 1968. In Unit 70o, Pilgrim Conglomerate Member of Colter Formation.

East Pilgrim 11, UWBM loc. C0239.—43°56.30′N, 110°33.00′W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake 7.5′ Quad, 1968. In Unit 5, Crater Tuff-Breccia Member of Colter Formation.

East Pilgrim 5, UWBM loc. C0240.—43°55.92′N, 110°33.23′W, unsurveyed, T. 46 N, R. 114 W, Teton County, Wyoming, Two Ocean Lake Quad, 1968. In Unit 28, Crater Tuff-Breccia Member of Colter Formation.

Emerald Lake SR, UWBM loc. C0241.—44°05.33′N, 110°18.90′W, unsurveyed, NW ¼ Sec. 33, T. 48 N, R. 112 W, Forest Service arbitrary grid, Teton National Forest Map, 1966, 15,400 feet (4,084 m) SSW of milepost 29 on south boundary of Yellowstone Park, Teton County, Wyoming, Mount Hancock 15′, 1959. Near Unit 1, Crater Tuff-breccia Member of Colter Formation.

The bones accumulated in three different depositional environments (Barnosky, 1983, 1984). Cunningham Hill (Unit O; UWBM loc. C0236) and North Pilgrim 2 (Unit 43; UWBM loc. C0237) represent portions of Miocene stream channels where pebble

Table 1.—*Fossil localities in the Colter Formation.*

Locality name	Locality number	Synonyms	Stratigraphic position (oldest at bottom)
Pilgrim Conglomerate Member			
Two Ocean Lake	UWBM loc. CO238	None	Unit 70o
Cunningham Hill	UWBM loc. CO236	KUVP loc. WYO 84	Unit O (=±69)
North Pilgrim 2	UWBM loc. CO237	None	Unit 43
Crater Tuff-Breccia Member			
East Pilgrim 5	UWBM loc. CO240	USNM—"S. Fork Pilgrim Creek, 5 mi. N. of Moran" KUVP loc. WYO 86 CMNH—"East Fork of Pilgrim Creek"	Unit 28
Roy Saunders Locality	None	None	Between Unit 5 and 28?
East Pilgrim 11	UWBM loc. CO239	None	Unit 5
Emerald Lake 1 SR	UWBM loc. CO241	AMNH—"SR near Emerald Lake on Fox Creek."	near Unit 1

sized bones and teeth were concentrated by currents. At Cunningham Hill, all material comes from a lense measuring about 2 m wide by 1 m deep (Pl. I, top). At North Pilgrim 2, fossils weather from a small scarp about 1 m wide by 3 m high (Pl. I, bottom). Most material came from slope wash at the base of these two localities. Fossils at East Pilgrim 5 (Unit 28; UWBM loc. C0240) and Two Ocean Lake (Unit 70o; UWBM loc. C0238) were preserved by volcanic ash falls. Bones at East Pilgrim 11 (Unit 5; UWBM loc. C0239) were incorporated into the base of an ash-flow.

SYSTEMATIC PALEONTOLOGY

Order Insectivora Illinger, 1811
Family Talpidae Fischer von Waldheim, 1817
Subfamily Talpinae Fischer von Waldheim, 1817
Tribe Scalopini Dobson, 1883
Genus **Domninoides** Green, 1956

Domninoides sp., cf. **D. storeri** Russell, 1976
Plate II A,B

Locality.—North Pilgrim 2, UWBM loc. C0237.
Age.—Late Barstovian.

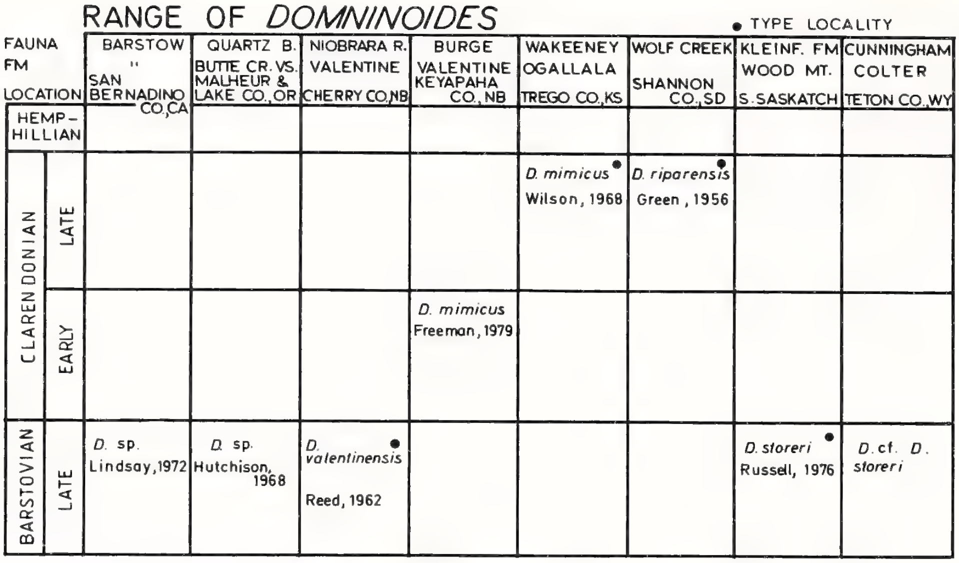
Range of genus.—Fig. 9.
Referred specimen.—M_3, UWBM 62728.
Measurements.—AP = 1.8 mm. TA = 1.2 mm. TP = 0.9 mm.

Description and comparison.—Terminology of talpid teeth follows that illustrated in Barnosky (1981:figs. 4, 6). UWBM 62728, an M_3, is referred to *Domninoides* on the bases of relatively small size and lingually open talonid basin (Pl. II A, B). UWBM 62728 shares these characters with the genotypic species, *D. riparensis* Green, 1956, and with all other species of the genus (Fig. 9). A wide anterior cingulum, characteristic of *Domninoides,* was apparently present on UWBM 62728 but has been broken.

UWBM 62728 differs from *Domninoides storeri* (Russell, 1976) only in slightly smaller size (0.3 mm shorter AP). Both show a small metastylid, which is absent in the smaller *D. riparensis* (AP = 1.5 mm) (Green, 1956:153–154). *D. valentinensis* (Reed, 1962:3) possesses a considerably larger M_3 (AP = 2.6 mm), as does *D. mimicus* (AP = 2.61–3.13 mm, Wilson 1968:108; Freeman, 1979:8). M_3's have not been reported from Barstow or Quartz Basin.

M_3's are larger in *Scalopus mcgrewi* (AP = 2.95–3.15 mm) (Voorhies, 1977:133), *Scapanus* (AP near 2 mm), *Proscalops tertius* (AP = 1.99–2.63 mm) (Bjork, 1975:810), *Proscalops secundus* (AP = near 2.1 mm), and *Proscalops evelynae* (AP = 2.2 mm) (MacDonald, 1963:169; Barnosky, 1982:1105). M_3 in *Oligoscalops* is smaller (AP = 1.5 mm) (Reed, 1961:475). *Neurotrichus* differs from UWBM 62728 in possessing a wider talonid neck. *Gaillardia* is distinct from UWBM 62728 in lacking connection between the metastylid and the metaconid (Hutchison, 1968:48).

Discussion.—UWBM 62728 cannot be differentiated from M_3's of *D. storeri.* In view of the meager record of *Dominoides,* however, referral to *D. storeri* is tentative.



RANGE OF *DOMNINOIDES*

● TYPE LOCALITY

		BARSTOW	QUARTZ B.	NIOBRARA R.	BURGE	WAKEENEY	WOLF CREEK	KLEINF. FM	CUNNINGHAM
FAUNA		BARSTOW	QUARTZ B.	NIOBRARA R.	BURGE	WAKEENEY	WOLF CREEK	KLEINF. FM	CUNNINGHAM
FM		"	BUTTE CR. VS.	VALENTINE	VALENTINE	OGALLALA		WOOD MT.	COLTER
LOCATION		SAN BERNADINO CO,CA	MALHEUR & LAKE CO., OR	CHERRY CO,NB	KEYAPAHA CO., NB	TREGO CO.,KS	SHANNON CO.,SD	S.SASKATCH	TETON CO.,WY
HEMPHILLIAN									
CLARENDONIAN	LATE					*D. mimicus* ● Wilson, 1968	*D. riparensis* ● Green, 1956		
	EARLY				*D. mimicus* Freeman, 1979				
BARSTOVIAN	LATE	*D.* sp. Lindsay, 1972	*D.* sp. Hutchison, 1968	*D. valentinensis* ● Reed, 1962				*D. storeri* ● Russell, 1976	*D.* cf. *D. storeri*

Fig. 9.—Geographic and stratigraphic range of *Domninoides.*

Genus *Scalopoides* Wilson, 1960

Scalopoides, species indeterminate

Locality.—Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Range of genus.—Arikareean: Monroe Creek microfauna of Shannon County, South Dakota (MacDonald, 1972). Hemingfordian: Martin Canyon Quarry A of Logan County, Colorado (Wilson, 1960). Batesland fauna of Bennett County, South Dakota (Martin, 1976). Vedder fauna of Santa Barbara County, California (Hutchison and Lindsay, 1974). Late Barstovian: Quartz Basin, Red Basin faunas of Harney and Malheur Counties, Oregon (Hutchison, 1968). Kleinfelder Farm fauna of Saskatchewan (Storer, 1975). Late Clarendonian: Black Butte Fauna of Malheur County, Oregon (Hutchison, 1968).

Referred specimen.—M_3, UWBM 62829.

Measurement.—AP = 1.9 mm. TA = 1.2 mm. TP = 0.9 mm.

Description and comparison.—In size and general morphology UWBM 62829 resembles *Scalopoides ripafodiator* and *S. isodens* (Hutchison, 1968). A comparison to *Scapanoscapter* and *Achlyoscapter* is impossible because unworn M_3's of these genera are unknown. Unlike UWBM 62829, the metastylid and metaconid lack connection in *Gaillardia. Domninoides* differs from UWBM 62829 in lacking closure of the talonid basin. M_3 of *Mystipterus* is smaller (seldom exceeding 1.47 mm) than UWBM 62829, and additionally differs in having a basal cingulid. In *Neurotrichus,* the talonid is wider at the junction with the trigonid, in contrast to the narrow junction in the M_3 from Jackson Hole. M_3's with a less prominent metacristid than that in UWBM 62829 characterize *Scapanus.* In *Scalopus mcgrewi* the tooth is larger (AP = 2.95–3.15 mm) than the Jackson Hole specimen. M_3's smaller than UWBM 62829 occur in *Oligoscalops* (AP = 1.5 mm). *Proscalops* and *Domninoides* differ from UWBM 62829 because the talonid opens lingually; the talonid basin is closed lingually in the Jackson Hole specimen. In *Mesoscalops* the tooth is more hyposodont than in UWBM 62829.

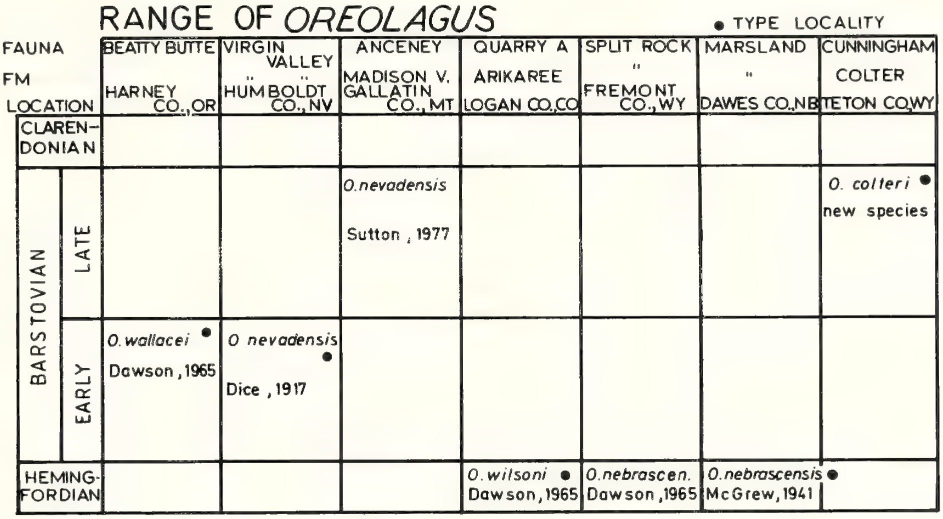
Scalopini, species indeterminate

Scalopoides, Sutton and Black, 1972.

Locality.—Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Referred specimens.—M^1, UWBM 62831. M_1 or M_2 fragment, KUVP 17489. M^2 fragment, KUVP 17488.

Description and comparison.—UWBM 62831 resembles the M^1 of *Achlyoscapter longirostris* (Hutchison, 1968:fig. 84) in size and general morphology. M^1 in *Scalopoides, Scapanoscapter,* and known *Domninoides* are larger (2.3 mm or more AP). *Scalopoides* further differs in possessing a well defined parastyle, in contrast to the small one in UWBM 62831. Specimens of *Scapanoscapter* (Hutchison, 1968:fig. 72) possess a more pronounced protoconule (=paraconule of Hutchison). The mesostyle in the Jackson Hole specimen closely resembles that of *Scalopoides*; the mesostyle is shorter in *Achlyoscapter.* Unlike the condition in *Mystipterus,* the posterior border of M^1 is not concave in any of these forms. UCMP 78774 from the Barstow Formation



RANGE OF *OREOLAGUS*

● TYPE LOCALITY

FAUNA		BEATTY BUTTE	VIRGIN VALLEY	ANCENEY	QUARRY A	SPLIT ROCK	MARSLAND	CUNNINGHAM
FM			" "	MADISON V.	ARIKAREE	"	"	COLTER
LOCATION		HARNEY CO., OR	HUMBOLDT CO., NV	GALLATIN CO., MT	LOGAN CO., CO	FREMONT CO., WY	DAWES CO., NB	TETON CO., WY
CLAREN-DONIAN								
BARSTOVIAN	LATE			O. nevadensis Sutton, 1977				O. colteri ● new species
	EARLY	O. wallacei ● Dawson, 1965	O nevadensis ● Dice, 1917					
HEMING-FORDIAN					O. wilsoni ● Dawson, 1965	O. nebrascen. Dawson, 1965	O. nebrascensis ● McGrew, 1941	

Fig. 10.—Geographic and stratigraphic range of *Oreolagus.*

resembles the Jackson Hole specimen in general morphology but is larger (AP = about 2.8 mm).

KUVP 17488, a fragment of M^2, differs from that in *Scalopoides* in possessing a prominent metastyle located just anterior to the posterior margin of the tooth. The metastyle projects straight labiad. Like that in *Scalopoides isodens,* the mesostyle of KUVP 17488 shows no trace of division. The tooth is unknown in *Scapanoscapter* or *Achlyoscapter.* The mesostyle is divided in *Domninoides.*

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus ***Oreolagus*** Dice, 1917

Oreolagus colteri, new species
Plate III A–H, J

Holotype.—UWBM 62698, P^4 or M^1.

Hypodigm.—UWBM 62698, 62694, 62701, 62702, 62707, 62709, 62711 (P^3). UWBM 62704, 62708, 62720, 62722, 62715 (P^4 or M^1). UWBM 62714, 62717 (M^2). UWBM 62718, 62719 (P_3). UWBM 62712, 62721 (P_4 or M_1).

Type locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—For John Colter, an early trapper in Jackson Hole.

Age.—Late Barstovian.

Range of genus.—Fig. 10.

Referred specimens.—DP_3, UWBM 62697. DP_4, UWBM 62729. DP^2, UWBM 62815, 62817. Upper DP fragment, KUVP 17820. Lower molariform teeth, UWBM 62716, 62695, 62651, 62816. P^4 or M^1, UWBM 62818. UWBM 62815 through 62818 and KUVP 17820 from UWBM loc. C0236, others from type locality.

Diagnosis.—Small, with P^3 seldom exceeding 2.4 mm wide, P^4–M^1 usually less than 2.7 mm wide. P^3 with anteroloph less than ½ width of tooth. P^4–M^1 with prominent crescentic valley, hypostria not exceeding ¾ transverse width of tooth, two rudimentary root-bumps near occlusal surface labially. DP_3 with single groove bifurcating anterior surface of tooth. P_3 with lingual accessory groove sometimes present.

Description and comparison.—Cheek teeth from Jackson Hole match in all respects the generic characters of *Oreolagus* (Dawson, 1965:29), including absence of roots, and simplification of M^2 into a single, transversely elongate, basined column. The simplification implies loss of M^3 although no palates were recovered. These characters differentiate *Oreolagus* from *Desmatolagus, Gripholagomys, Hesperolagomys, Russellagus,* and *Cuyamalagus,* in which M^3, complexity in M^2, and roots are retained.

In the Jackson Hole species, the anteroloph of P^3 (Pl. IIIF) reaches less than halfway across the tooth (Table 2), as in *O. wallacei* and the Anceney specimens referred to *O. nevadensis* by Sutton (1977). The anterolophs extend half the width of the premolar in *O. wilsoni* and *O. nebrascensis.* All of the Jackson Hole specimens are shorter anteroposteriorly than the single P^3 of *O. wilsoni* reported by Dawson (1965:6, KUVP 10303, ratio AP/T = 0.61), and three of the six are more anteroposteriorly compressed relative to width (Table 2). Two specimens

Table 2.—*Dental measurements,* Oreolagus colteri, *new species, Colter Formation.*

Locality	Specimen	AP	Width anteroloph	T	AP/T
		P^3			
NP	UWBM 62693	1.3	0.8	1.9	0.68
NP	UWBM 62694	1.3	1.0	2.4	0.54
NP	UWBM 62701	1.2	0.7	2.1	0.57
NP	UWBM 62707	1.3	1.1	2.3	0.57
NP	UWBM 62709	1.3	1.0	2.0	0.65
NP	UWBM 62711	1.2	0.8	1.8	0.67
		AP	Width hypostria	T	AP/T
		P^4 or M^1			
NP	UWBM 62698	1.2	1.3	2.3	0.52
NP	UWBM 62704	1.5	1.2	2.7	0.56
NP	UWBM 62708	1.3	1.2	2.5	0.52
NP	UWBM 62720	1.4	1.4	2.2	0.64
CH	UWBM 62818	1.3	0.8	2.5	0.52
NP	UWBM 62715	1.5	0.8	—	—
NP	UWBM 62722	1.5	0.9	2.3	0.65
		M^2			
NP	UWBM 62714	1.0	—	1.7	0.59
NP	UWBM 62717	1.0	—	1.9	0.53
		AP	TA	TP	
		P_3			
NP	UWBM 62718	1.2	1.0	1.5	
NP	UWBM 62719	1.1	1.1	1.3	
		P_4 or M_1			
NP	UWBM 62721	1.5*	1.8	1.7	
NP	UWBM 62712	1.8	1.7	—	
		dP_4			
NP	UWBM 62723	1.8	1.2	1.4	
		dP_3			
NP	UWBM 62697	—	—	1.4	
		dP^2			
		AP		T	
CH	UWBM 62817	1.1		1.9	

* At least.
NP North Pilgrim 2.
CH Cunningham Hill.

of *O. nebrascensis* from Split Rock resemble *O. wilsoni* in these respects (CMNH 13750, UWYO 1952, AP/T = 0.61 and 0.63). P^3 in *O. wallacei* is slightly larger and more anteroposteriorly compressed than the Jackson Hole material (AP/T = 0.51, LACM CIT 3074, Dawson, 1965:27). The P^3's from Anceney, CMNH 28533, 28538, 28686 (Sutton, 1977), resemble those of *Oreolagus* from Jackson Hole in size and fall within the range of anteroposterior compression (AP/T = 0.63, 0.68, 0.58). As in the other species, none of the P^3's of *O. colteri* show traces of roots.

The similarity of seven isolated teeth suggest that P^4 and M^1 of *O. colteri* are nearly identical in occlusal morphology. Given an equal chance of preservation and recovery for P^4 and M^1, the probability that any tooth is P^4 is 0.50. Likewise, the probability that any tooth is M^1 is 0.50. The probability that all seven teeth are P^4's or all seven teeth are M^1's is therefore $0.50^7 = 0.008$. Size differences should not bias the sample because these teeth are of similar dimensions in other species and relatively small M^2's and P_3's were recovered.

A prominent crescentic valley characterizes all teeth from Jackson Hole (Pl. III A, G), but is lacking in M^1's of *O. wallacei* and Sutton's sample from Anceney. Like *O. wilsoni,* the hypostria in the Jackson Hole teeth extends from $\frac{2}{5}$ to $\frac{3}{5}$ across the width of the tooth, which contrasts with that of M^1's from Anceney, *O. nebrascensis,* and *O. wallacei* ($\frac{3}{4}$ to $\frac{4}{5}$). Judging from the usual condition in *Oreolagus,* teeth from Jackson Hole with a short hypostria (0.8–0.9 mm) are probably P^4's, whereas those with long ones (1.2–1.4 mm) most likely represent M^1's. The hypostria persists throughout wear and, depending on wear-stage, short hypostria either abut the lingual edge of the crescentic valley (moderate wear) or terminate 1 to 3 mm from the valley (later wear stages). Long hypostria generally extend past the anterior part of the crescentic valley by about 1 mm (Pl. III A, B, G), except in the most advanced wear stages when they may stop as much as 0.2 mm short of the valley. Undescribed in any other species are two rudimentary root swellings that are homologous with roots of more primitive genera and occur labially near the occlusal surface (Pl. III D, E). In size, the P^4's and M^1's are slightly smaller than in *O. wilsoni* (AP = 1.5–1.6 mm, T = 2.9 mm) and *O. wallacei* (AP = 1.6–1.7 mm, T = 2.7–2.8 mm) (Dawson, 1965), but resemble *O. nebrascensis* from Split Rock.

In general morphology, the worn M^2's of *O. colteri* (Pl. III H) closely approximate those of *O. wallacei* and *O. nebrascensis* from Split Rock. M^2's of *O. colteri* (Table 2) however, are smaller than in *O. wallacei,* most *O. nebrascensis,* and *O. wilsoni,* in which dimensions range from 1.0–1.2 mm AP and 2.1–2.3 mm T. The lingual fold is distinct in the Jackson Hole material, more like *O. nebrascensis* than *O. wallacei.*

One of the two P_3's from Jackson Hole has a very shallow accessory lingual fold that is filled with cement. Such folds occur in *O. wilsoni* and *O. nebrascensis* but not in *O. nevadensis.* As is usual in *Oreolagus,* a short protoloph, long posterior loph, and prominent labial groove characterize these teeth. Lower molariform teeth are fragmented and therefore cannot be differentiated from those of other species.

The DP^2 of *O. colteri,* with an extremely shallow hypostria that disappears when the tooth wears about half-way, possesses a prominent lingual root and a smaller labial one. The lingual root is squarer than in *O. wilsoni* but different wear-stages preclude other comparisons. The hypostria and lingual notch are slightly less pronounced in a figure of *O. nebrascensis* from Split Rock (FMNH PM2219, Dawson, 1965). A deciduous P_3 from Jackson Hole (Pl. III J), missing its posterior third, differs from that in *O. nebrascensis* and *O. wilsoni* in possessing a median groove on the anterior margin of the tooth, rather than a median lobe bordered on each side by grooves (see Dawson, 1965:fig. 28). Strong anterior and posterior roots occur on DP_4. The talonid is expanded more anteroposteriorly than the trigonid, but in *O. nebrascensis* from Split Rock the trigonid is more expanded.

Discussion.—*Oreolagus colteri* of Jackson Hole is relatively primitive in possession of rudimentary root-bumps on P^4 and M^1 and apparent retention of crescentic valleys on M^1. Such features were previously known only in Hemingfordian species. *O. colteri* differs from these geologically older forms, however, in smaller size, configuration of DP_3, and short anteroloph on P^3. It shares the short anteroloph on P^3 with all Barstovian *Oreolagus* (Anceney, *O. nevadensis, O. wallacei*) and small size with two of the three. In these respects morphology of *O. colteri* seems to be somewhat intermediate between that of previously described Hemingfordian and Barstovian species.

Family Leporidae Gray, 1821
Subfamily Archaeolaginae Dice, 1929
Genus ***Hypolagus*** Dice, 1917

Hypolagus, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to late Blancan of western North America, mid-Pliocene(?) of Asia, Villafranchian of Asia and Europe (Dawson, 1958).

Referred specimens.—Lower M, KUVP 17818. P^2, UWBM 62696. Upper M, UWBM 62699, 62700, 62706, 62710, 62713, KUVP 17816, 17817, 65679. KUVP specimens from UWBM loc. C0236, others from loc. C0237.

Measurements.—Table 3.

Table 3.—*Dental measurements,* Hypolagus *and* Archaeolagus emeraldensis, *new species, Colter Formation.*

Tooth	Specimen	AP	TA	TP	T
	Archaeolagus emeraldensis				
P_3	AMNH 89726	2.8	—	2.1	—
P_4	AMNH 89801	2.7	2.7	2.6	—
M_1	AMNH 89801	2.9	2.9	2.7	—
M_2	AMNH 89801	3.0	2.7	2.6	—
	Hypolagus, species indeterminate				
P^2	UWBM 62696	1.1	—	—	1.9
M*	UWBM 62699	1.4	—	—	2.5
M*	UWBM 62700	1.5	—	—	2.6
M*	UWBM 62713	1.4	—	—	2.5

* Molariform upper tooth.

Discussion.—Because most of the teeth are broken and worn, and P_3 is not represented, species determination was not possible. The well developed reentrant and shallow external groove on the anterior surface of P^2, combined with slightly crenulated hypostria on some molariform teeth, identify the genus as *Hypolagus.*

Archaeolagus emeraldensis, new species
Plate III I, K

Holotype.—AMNH 89726, P_3.

Hypodigm.—AMNH 89801, mandible with P_4–M_2.

Type locality.—Emerald Lake SR, UWBM loc. C0241.

Etymology.—For type locality.

Age.—Late Arikareean.

Range of other named species of genus. Arikareean: John Day Formation of northeast Oregon (*A. ennisianus* Cope, 1881) (Dawson, 1958). Tick Canyon fauna of southern California (*A. acaricolus* Dawson, 1958) (Whistler, 1967). Late Arikareean: Standing Rock local fauna northwest of Albuquerque, New Mexico (*A.* cf. *A. macrocephalus*) (Gawne, 1976). Hemingfordian: Rosebud Formation of Wounded Knee area, South Dakota (*A. macrocephalus Matthew,* 1907; *A. primigenius* Matthew, 1907) (Dawson, 1958; MacDonald, 1963).

Referred specimens.—Holotype and paratype only known specimens.

Diagnosis.—Larger than *A. acricolus* and *A. ennisianus,* smaller than average *A. macrocephalus* (see Fig. 11 and Table 3). P_3 more elongate than in *A. primigenius, A. macrocephalus,* and *A. acaricolus,* with ratio AP/T near 1.33, anteroexternal groove facing more labiad than in *A. primigenius.* P_4–M_2 talonids wide, with ratio of trigonid width/talonid width commonly between 1.0 and 1.1.

Description and comparison.—Lower cheek teeth

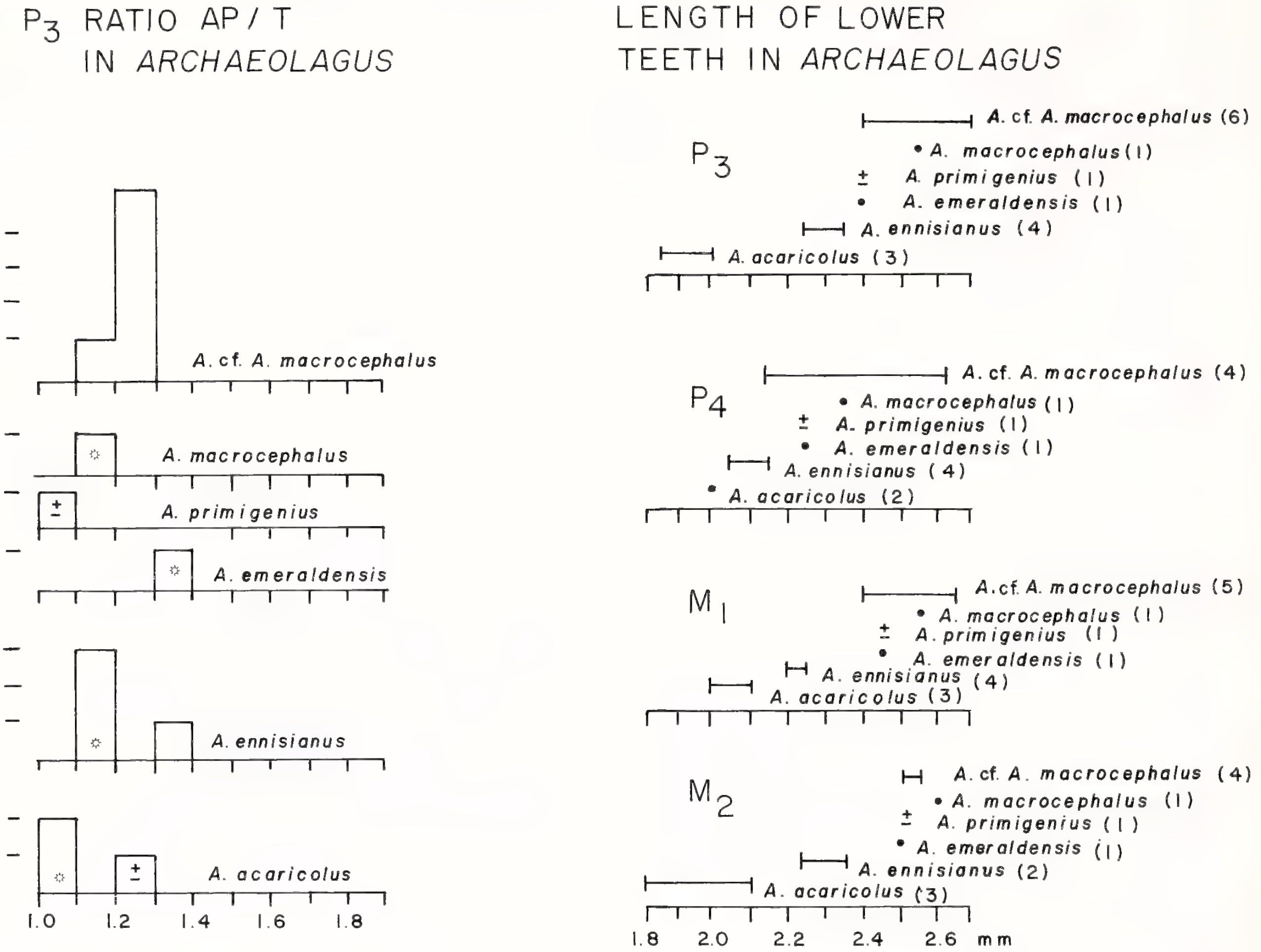
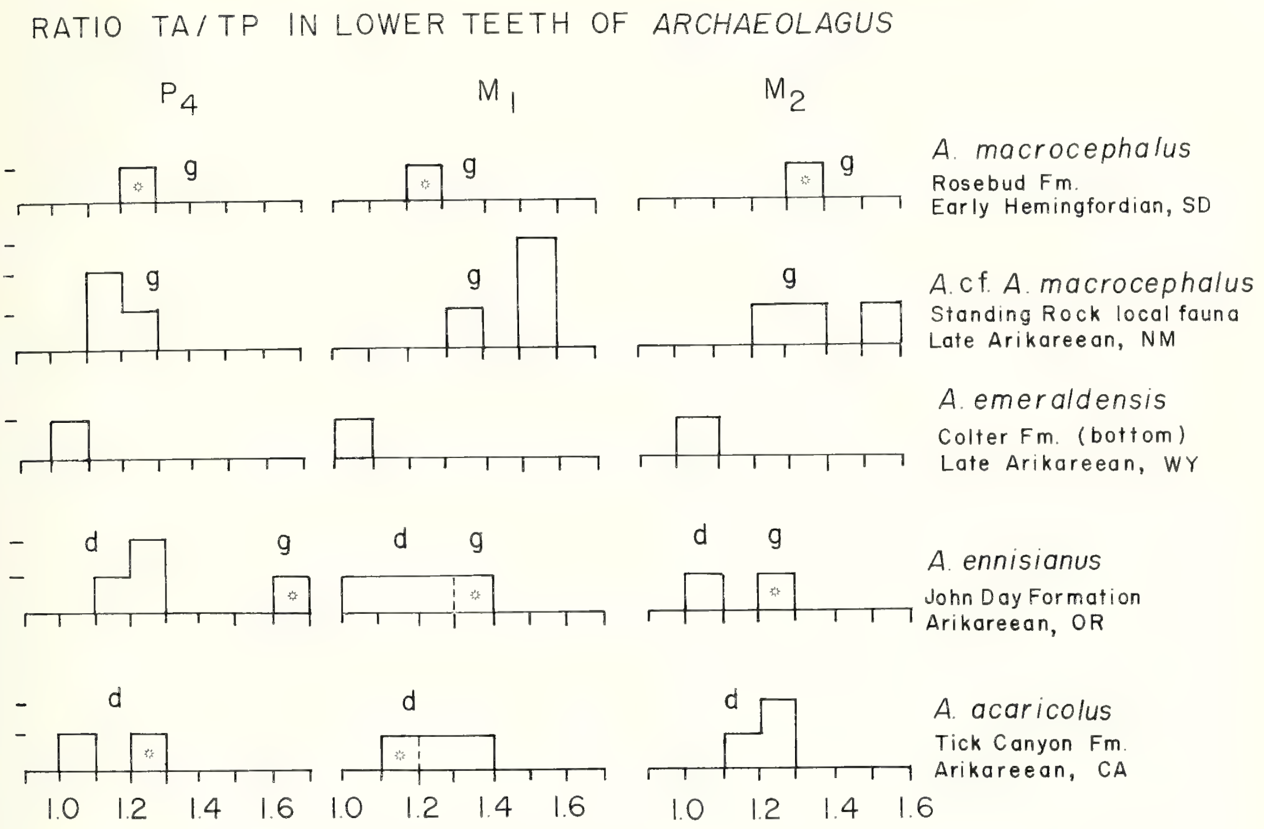


Fig. 11.—*Left:* Comparisons of the ratio AP/T in species of *Archaeolagus. Right:* Comparisons of the length of lower cheekteeth in species of *Archaeolagus.* Bars illustrate the observed range; the number of measured specimens is shown in parentheses. Data for *A.* cf. *A. macrocephalus, A. macrocephalus,* and the type of *A. ennisianus* from Gawne (1976); for others except *A. emeraldensis* from Dawson (1958). A star indicates a type specimen.

of *A. emeraldensis* (Pl. III I, K) are larger than those of *A. acaricolus* and *A. ennisianus* but somewhat smaller than usual for *A. macrocephalus* and *A.* cf. *A. macrocephalus* (Fig. 11). As in *A. ennisianus,* the P_3 is long (Fig. 11) with a shallow anteroexternal groove that faces mainly labiad. The portion anterior to this groove is shorter in three specimens of *A.* cf. *A. macrocephalus* figured by Gawne (1976), and P_3 as a whole is relatively shorter in these and in the type of *A. macrocephalus* (Fig. 11). Even shorter P_3's, with the anteroexternal groove facing more anterad, characterize *A. primigenius* and *A. acaricolus* (Dawson, 1958). The posteroexternal reentrant, which is the only external groove filled with cement, extends about halfway across the tooth in *A. emeraldensis.* The P_3 differs from those of Paleolaginae in possessing more than one external groove, and from *Hypolagus* in lacking a relatively deep and cement-filled anteroexternal groove.

P_4–M_2 (Pl. III I) of *A. emeraldensis* show the general leporid pattern, but relatively wide talonids make them distinct from most other species (Fig. 12). A P_4 of *A. acaricolus* (LACM CIT 5172) and an M_2 of *A. ennisianus* (YPM unnumbered, Dawson, 1958) resemble the Emerald Lake specimen. On M_2, the lingual margin of the talonid is nearly twice as long as the labial margin.

Discussion.—In its larger size *A. emeraldensis* may be slightly more advanced than *A. ennisianus,* but the long P_3 and wide talonids suggest a relatively close relationship between the two. Because *A. macrocephalus* and *A.* cf. *A. macrocephalus* both share even larger size and narrow talonids, these species seem to be farther removed. *Archaeolagus acari-*



Sources for comparative measurements: d = Dawson (1958), g = Gawne, (1976). *Type specimen.

Fig. 12.—Comparison of the ratios TA/TP for lower teeth in species of *Archaeolagus.*

colus shows least similarity to *A. emeraldensis,* judging from the short P_3 and small size. *A. primigenius,* by virtue of the short P_3, appears more closely related to *A. acaricolus* than to *A. emeraldensis.*

AMNH 89801 and the type of *A. emeraldensis* may represent the same individual, because the teeth are similarly worn and the P_3 fits well into the portion of the alveolus that remains in AMNH 89801. The paucity of fossils at the very small exposure increases the likelihood that only one individual is represented.

Order Rodentia Bowditch, 1821
Family Sciuridae Gray, 1821
Subfamily Sciurinae Baird, 1857
Genus **Spermophilus** Cuvier, 1825

***Spermophilus* (*Otospermophilus*)**, near
S.* (*O.*) *primitivus Bryant, 1945
Plate II J–L

Locality.—North Pilgrim 2, UWBM loc. C0237.
Age.—Late Barstovian.

Range of morphologically similar species.—Fig. 13.

Referred specimens.—M_1 or M_2, UWBM 62733, 62739. M_3, UWBM 62742, 62736, 62741. M^1 or M^2, UWBM 62737, 62740, 62746.

Measurements.—Table 4 and Black (1963), Storer (1975), Lindsay (1972), and Barnosky (1983).

Description and comparison.—The molars from Jackson Hole are larger than those of *Tamias* and *Miosciurus,* but smaller than in *Protosciurus, Palearctomys, Arctomyoides, Paenemarmota, Marmota, Protospermophilus,* and most species of *Spermophilus* (Black, 1963). *Ammospermophilus* differs in having an M_3 commonly wider than long, and on M^{1-2} a constriction separating the metaloph from the protocone. Species with molars similar in size to the Jackson Hole material include *Spermophilus primitivus,* which is only slightly larger (lower molars 2.1–2.7 mm AP, Black, 1963), *S. tephrus* (Black, 1963), *S.* sp. from Kleinfelder Farm (Storer, 1975), *Miospermophilus bryanti* (Black, 1963), and *M.* sp. from Barstow (Lindsay, 1972). *S. tephrus* differs in possessing a large mesostyle located next to the

RANGE OF *SPERMOPHILUS* AND *MIOSPERMOPHILUS* ● TYPE LOCALITY

FAUNA FM LOCATION		BARSTOW " SAN BERNADINO CO., CA	SKULL SPG. (≈RED BASIN) MALHEUR CO., OR	RED BASIN BUTTE CR. VS. MALHEUR CO., OR	ANCENEY MADISON V. GALLATIN CO., MT	FLINT CREEK GRANITE CO., MT	QUARRY A ARIKAREE LOGAN CO., CO	SPLIT ROCK " FREMONT CO., WY	SNAKE CREEK " " SIOUX CO., NB	KLEINF. FM. WOOD MT S. SASKATCH.	CUNNINGHAM COLTER TETON CO., WY
HEMPHILLIAN									*S. matthewi* ● Black, 1961 Skinner, 1977		
CLARENDONIAN	LATE										
	EARLY										
BARSTOVIAN	LATE	*M.* sp. Lindsay, 1972	according to Shotwell, 1968 ↑?	*S. tephrus* Shotwell, 1968	*S.* sp. Sutton, 1977	*S. primitivus* ● Black, 1961, 1963				*S.* sp. Storer, 1975	*S.* near *S. primitivus*
	EARLY	*M.* sp. Lindsay, 1972	↑								
HEMINGFORDIAN			*S. tephrus* ● Black, 1963				*M. bryanti* ● Wilson, 1960 Black, 1963	*M. wyomingensis* Black, 1963 ● Munthe, 1979a			

Fig. 13.—Geographic and stratigraphic range of some Miocene species of *Spermophilus* and *Miospermophilus*.

metacone and a narrow anterior cingulum. In contrast, the Jackson Hole species has a small, centrally located mesostyle and an expanded anterior cingulum. The posterolingual corners of M_1 and M_2 show more reduction and rounding in *S.* sp. than in the teeth from Jackson Hole, judging from descriptions and illustrations by Storer (1975:74). *Miospermophilus wyomingensis* has sharp crests on lophs and cusps of upper molars, incomplete metalophids on M_1–M_2, and absence of metalophid on M_3. Fossils from Jackson Hole differ in having low rounded cusps and lophs, complete metalophid that isolates a small trigonid on M_1, and an incomplete but prominent metalophid on M_3. Unlike *M.* sp. from Barstow, an obvious parastyle occurs on M^1–M^2 of the Jackson Hole species, as does a mesostylid on M_1–M_2. The Jackson Hole species shares some characters with *M. bryanti,* but more with *S. primitivus,* and is therefore referred to *Spermophilus* (Table 5). Available material from Jackson Hole differs from *S. primitivus* in its distinctly smaller size and small rather than large mesostyle, and it may therefore represent a new species. The *Spermophilus* from Anceney, reported in an unpublished doctoral dissertation by Sutton (1977), resembles the Jackson Hole material except for slightly larger size.

Discussion.—Small size, moderately well developed metalophids, and only slight curvature of the entoconid area in the Jackson Hole specimens resemble conditions in primitive species of *Spermophilus.* The two species that bear closest resemblance, *S. primitivus* of the Flint Creek fauna and *S.* sp. from Anceney, are both from Rocky Mountain deposits of late Barstovian age.

Tamias Illinger, 1811

Tamias cf. *T. ateles* (Hall), 1930

Miospermophilus Sutton and Black, 1972.

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of species.—Late Barstovian: Barstow fauna of San Bernardino County, California (Lindsay, 1972). Tonapah fauna of Nye County, Nevada (Black, 1963; Henshaw, 1942). Early Clarendonian: Matthews Ranch fauna of the Cuyama Badlands, Cal-

Table 4.—*Dental measurements,* Spermophilus *near* S. primitivus, *Colter Formation, North Pilgrim 2.*

Tooth	Specimen	AP	T	AP/T
$M^{1\text{ or }2}$	UWBM 62740	1.7	2.2	0.77
$M^{1\text{ or }2}$	UWBM 62746	1.8	2.2	0.87
$M^{1\text{ or }2}$	UWBM 62737	1.6	—	—
$M_{1\text{ or }2}$	UWBM 62739	1.5	1.9	0.79
$M_{1\text{ or }2}$	UWBM 62733	—	2.1	—
M_3	UWBM 62741	2.0	1.8	1.11

Table 6.—*Dental measurements,* Tamias *cf.* T. ateles, *Colter Formation.*

Tooth	Specimen	AP	T	Locality
$M^{1\text{ or }2}$	UWBM 62836	1.3	1.6	Cunningham Hill
$M^{1\text{ or }2}$	UWBM 62834	1.4	1.7	Cunningham Hill
P_4	UWBM 62735	1.4	1.3	North Pilgrim 2
$M_{1\text{ or }2}$	UWBM 62835	1.4	1.7	Cunningham Hill
$M_{1\text{ or }2}$	KUVP 17487	1.4	1.7	Cunningham Hill
$M_{1\text{ or }2}$	UWBM 62734	1.3	1.5	North Pilgrim 2
M_3	UWBM 62738	—	1.4	North Pilgrim 2

ifornia (James, 1963). Late Clarendonian: Nettle Springs fauna of the Cuyama Badlands, California (James, 1963).

Referred specimens.—P_4, UWBM 62735. M_1 or M_2, UWBM 62734, 62735. M_3, UWBM 62738. M^1 or M^2, UWBM 62833, 62834, 62836. UWBM 62734, 62735, and 62738 from UWBM loc. C0237, others from loc. C0236.

Measurements.—Table 6.

Description and comparison.—These teeth are referred to *Tamias* on the basis of small size, very low and somewhat bulbous crowns, and marked anterior bowing of the anterior cingulid. *Miosciurus* differs in the less bowed anterior cingulid and more rounded posterolingual corner on lower molars (see Black, 1963:pl. 2, fig. 3). In *Ammospermophilus* of the Miocene, the protocone and metaloph tend to connect, especially in P^4 and M^1, the mesostyle is usually more prominent, and molars are usually slightly larger than in *Tamias* and teeth from Jackson Hole (James, 1963; Lindsay, 1972).

Upper molars from the Jackson Hole closely resemble those of *T. ateles,* which have been described in detail by Black (1963) and Lindsay (1972). In the only complete and unworn specimen of M^1 or M^2, the mesostyle is slightly smaller and the anterior cingulum is less expanded than in the type specimen. In view of these minor differences, referral to *T. ateles* is tentative. Lower molars are nearly identical to *T. ateles* from Tonapah figured by Black (1963: pl. 2, fig. 2).

Tamias sp. from the Arikareean Sharps Formation (Black, 1963), Hemingfordian Thomas Farm fauna of Florida, and Hemingfordian Martin Canyon Quarry A fauna show stronger union of the metaloph and protocone. In *T. ateles, T.* sp. from Kleinfelder Farm (Storer, 1975:fig. 53g), and *Tamias* of the Colter Formation, the two structures do not meet. A less reduced posterolingual portion of the M_1–M_2 differentiates the Kleinfelder form and the Split Rock *T.* sp. from the Colter material.

Subfamily Petauristinae Simpson, 1945
Genus *Petauristodon* Engesser, 1979

***Petauristodon,* species indeterminate**
Plate II M

Locality.—North Pilgrim 2, UWBM loc. C0237.

Age.—Late Barstovian.

Range of genus.—Fig. 14.

Referred specimen.—M_3, UWBM 62743.

Measurements.—AP = 3.2 mm. T = 3.3 mm.

Table 5.—*Comparison of* Spermophilus *from Colter Formation,* Miospermophilus bryanti, *and* Spermophilus primitivus.

1. Characters shared by all three species	
a. Size (*S. primitivus* slightly larger)	
b. High parastyles	
c. Wide anterior cingulum	
d. Metaloph joins protocone obliquely	
e. Corner of entoconid slightly curved	
2. Characters shared by Jackson Hole species and *S. primitivus*	2. Condition in *M. bryanti*
a. Posterolophid low	a. Posterolophid high
b. Distinct mesostylid and mesoconid although slightly less in Jackson Hole species	b. Mesostylid small, mesoconid absent
c. Metalophid weak, isolates small trigonid basin on M_1 but not on M_2	c. Trigonid basin isolated on both M_1 and M_2
3. Characters shared by Jackson Hole species and *M. bryanti*	3. Condition in *S. primitivus*
a. Mesostyle small	a. Mesostyle large

RANGE OF *PETAURISTODON*

● TYPE LOCALITY

FAUNA		BARSTOW	DOME SPRING	MATTHEWS RCH.	NETTLE SPRING	RED BASIN	KLEINF. FM.	CUNNINGHAM
FM		"	CALIENTE	CALIENTE	CALIENTE	BUTTE CR. VS.	WOOD MT.	COLTER
LOCATION		SAN BERNADINO CO., CA	CUYAMA VALLEY, CALIFORNIA			MALHEUR CO., OR	S. SASKATCH.	TETON CO., WY
HEMPHILLIAN								
CLARENDONIAN	LATE				*P. matthewsi* ● James, 1963			
	EARLY			*P. matthewsi* *P.* sp. James, 1963				
BARSTOVIAN	LATE	*P. jamesi* ● *P. minimus* ● Lindsay, 1972	*P. uphami* ● James, 1963			*P.* sp. Shotwell, 1968	*P.* sp. Storer, 1975	*P.* sp.

Fig. 14.—Geographic and stratigraphic range of *Petauristodon.*

Description and comparison.—Lophids in the central basin of UWBM 62743 (Pl. II M) are better defined than in the only other complete M_3 that has been described, that of *P. matthewsi.* The Jackson Hole species further differs from *P. matthewsi,* as well as from *P.* sp. of Kleinfelder Farm, in having a larger M_3. The M_3 of *P. jamesi,* from which the anterior third is broken, has a less expanded posterointernal margin than the Jackson Hole specimen. Although M_3 is unknown for *P.* sp. of Red Basin, it was probably larger than UWBM 62743; the P_4's from Red Basin range from 3.48 to 4.23 mm in width. The Jackson Hole form cannot be differentiated from *P.* sp. of Matthews Ranch, in which morphology of the worn M_1–M_2 falls within the range to be expected in the dentition represented by UWBM 62743. *P. uphami* is known only by upper teeth.

Sciuridae, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Referred specimens.—Molar fragments, KUVP 65678 from UWBM loc. C0236, UWBM 62747 from loc. C0237.

Discussion.—Both specimens are much larger than molars of *Spermophilus primitivus,* but too worn and broken for even generic assignment.

Family Aplodontidae Troussart, 1897
Subfamily Allomyinae Marsh, 1877
Genus *Allomys* Marsh, 1877

Allomys cristabrevis, new species
Plate II C

Holotype.—AMNH 89727, M_1.

Type locality.—Emerald Lake SR, UWBM loc. C0241.

Etymology.—Crista (crest) and brevis (short) referring to the diagnostically short, blunt crests.

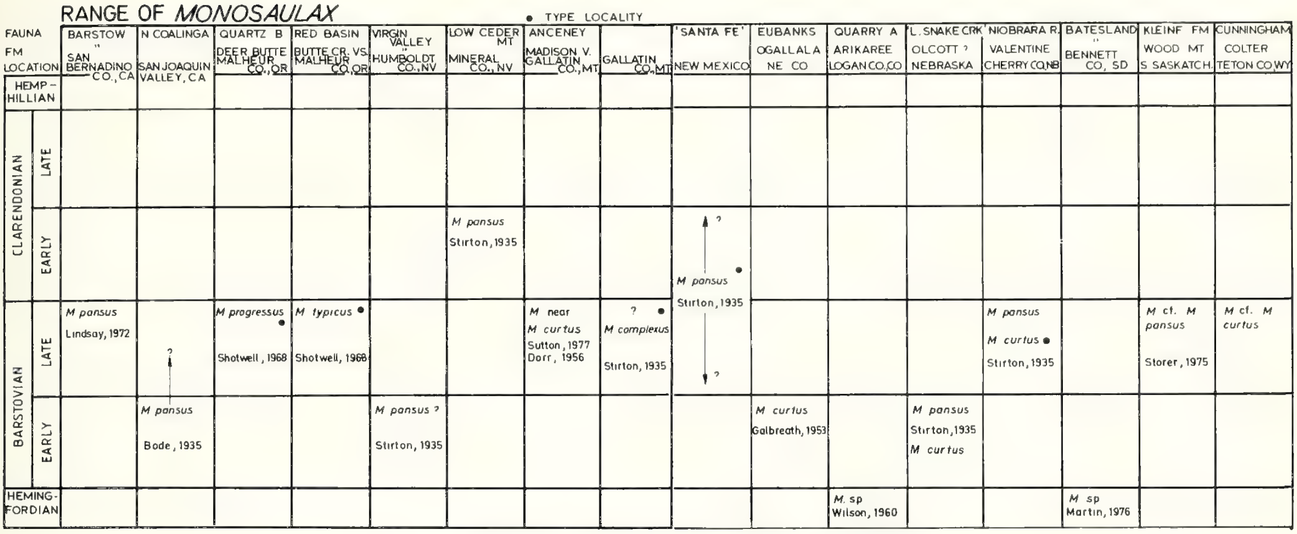
Age.—Late-early Arikareean.

Range of most closely related species.—Late-early Arikareean (*Meniscomys* Concurrent-range Zone): fauna of Monroe Creek Formation from Wounded Knee area, South Dakota (*Allomys harkseni* MacDonald, 1963) (J. R. MacDonald, 1970; L. J. MacDonald, 1972). John Day Formation, central Oregon (*Allomys cavatus* Cope, 1881) (Rensberger, 1983).

Referred specimens.—Type only known material.

Diagnosis.—M_1 (only known tooth) large (2.7 mm AP), metaconid positioned near center of anterior border, internal crests more blunt than in any other species, extending less far toward center of tooth than in other species except *A. cavatus,* posterolabial fossettid not fully formed.

Description and comparison.—As in all M_1's of *Allomys* the crests in AMNH 89727 are more prominent than in *Parallomys* Rensberger, 1983, but low-



RANGE OF *MONOSAULAX*

● TYPE LOCALITY

FAUNA FM LOCATION		BARSTOW " SAN BERNADINO CO., CA	N COALINGA SAN JOAQUIN VALLEY, CA	QUARTZ B DEER BUTTE MALHEUR CO., OR	RED BASIN BUTTE CR. VS. MALHEUR CO., OR	VIRGIN VALLEY " HUMBOLDT CO., NV	LOW CEDER MT MINERAL CO., NV	ANCENEY MADISON V. GALLATIN CO., MT	GALLATIN CO., MT	'SANTA FE' NEW MEXICO	EUBANKS OGALLALA NE CO	QUARRY A ARIKAREE LOGAN CO., CO	L. SNAKE CRK OLCOTT ? NEBRASKA	NIOBRARA R. VALENTINE CHERRY CO., NB	BATESLAND " BENNETT CO., SD	KLEINF FM WOOD MT S SASKATCH.	CUNNINGHAM COLTER TETON CO., WY
HEMPHILLIAN																	
CLARENDONIAN	LATE																
	EARLY						*M pansus* Stirton, 1935			↑ ? *M pansus* ● Stirton, 1935 ↓ ?							
BARSTOVIAN	LATE	*M pansus* Lindsay, 1972	? ↑	*M progressus* ● Shotwell, 1968	*M typicus* ● Shotwell, 1968			*M* near *M curtus* Sutton, 1977 Dorr, 1956	? ● *M complexus* Stirton, 1935					*M pansus* *M curtus* ● Stirton, 1935		*M* cf. *M pansus* Storer, 1975	*M* cf. *M curtus*
	EARLY		*M pansus* Bode, 1935			*M pansus* ? Stirton, 1935					*M curtus* Galbreath, 1953		*M pansus* Stirton, 1935 *M curtus*				
HEMINGFORDIAN												*M.* sp Wilson, 1960			*M* sp Martin, 1976		

Fig. 15.—Geographic and stratigraphic range of *Monosaulax.*

er than in *Alwoodia magna* Rensberger, 1983. Unlike *Alwoodia magna* and most *Allomys,* however, the internal crests are more blunt in *A. cristabrevis,* much like the condition in *A. cavatus.*

In contrast to *Allomys cavatus, A. simplicidens* Rensberger, 1983, *A. reticulatus* Rensberger, 1983, and *A. tessellatus* Rensberger, 1983, the M_1 of *Allomys cristabrevis* is large, measuring 2.7 mm AP × 2.4 mm T. It further differs in location of the metaconid near the center of anterior border. In the other four species, the metaconid is positioned near the lingual margin of the tooth. The M_1 of *A. nitens,* evidenced by UCMP 107717, UWBM 58058, and UWBM 51967, somewhat resembles the Jackson Hole specimen in size and less lingual position of the metaconid. Even in these specimens, however, the metaconid is more lingually positioned. The M_1 in *A. nitens, A. cavatus, A. simplicidens, A. reticulatus,* and *A. tessellatus* shows a flat lingual margin, unlike the bulging margin of the M_1 in *A. cristabrevis.* The same species differ from *A. cristabrevis* in having a crest that connects the mesoconid and hypoconulid to isolate a lake near the hypoconid. The crests are too short to isolate a lake on M_1 of *A. cristabrevis. Alwoodia magna* resembles the Jackson Hole specimen in the bulging lingual margin, but resembles the other species of *Allomys* in the possession of a hypoconid lake and connection of the metaconid and entoconid by a minor crest. The M_1 of one specimen of *Allomys harkseni,* SDSM 6273 (MacDonald, 1970), is very similar to the Jackson Hole specimen, differing only in the slightly longer crest emanating from the metaconid, longer posterior arm of the protoconid, and slightly more elongate mesoconid that isolates a hypoconid lake after considerable wear. Four other M_1's (LACM 120347, 120348, 120352, 120353, reported as LACM 23525, 23526 in MacDonald, 1972) of *A. harkseni* additionally differ in the prominent junction of the mesoconid and hypoconid crests as well as anterior extension of the hypoconulid. Because of these longer crests, 3 lakes occur when the posterior half of the tooth is worn, unlike the single transversely elongate lake in *A. cristabrevis.* Other M_1's of "*A. harkseni*" reported by MacDonald (1970) and MacDonald (1972) from LACM loc. 1871 differ considerably in the thinner, more convoluted crests.

Discussion.—AMNH 89727 most closely resembles two species that occur in the *Meniscomys* Concurrent-range zone. Except for slight advancement in central extension of crests, referred teeth of *Allomys harkseni* from the upper part of the zone (Monroe Creek Formation) are virtually identical to the M_1 of *Allomys cristabrevis.* The species are particularly similar in the labial position of the metaconid, bulging lingual margin, blunt crests, and large size. The Jackson Hole species is probably slightly older, perhaps equating with the middle of the *Meniscomys* Concurrent-range Zone, because the blunt shorter crests are a primitive feature that indicate an earlier stage in heightening and extending internal crests toward the middle of the tooth. Rensberger (1982, 1983), in thoroughly documenting evolutionary sequences in allomyines, cited blunt short crests as a primitive character. In the John Day Formation, only *Allomys cavatus* has crests as blunt and short as *A. cristabrevis,* but is slightly more advanced in closure of the hypoconid lake and somewhat flatter lingual margin. The type locality for *A. cavatus* is not known, but probably occurs below the middle of the *Meniscomys* Concurrent-range Zone (Rensberger, 1983). *Alwoodia magna,* the only North American allomyine with which *Allomys cristabrevis* and *Allomys harkseni* share the primitive feature of a lingually convex M_1, is restricted to the lower part of the *Meniscomys* Concurrent-range Zone in the John Day Formation.

Subfamily Meniscomyinae Rensberger, 1981

Genus ***Niglarodon*** Black, 1961

Niglarodon **sp.**

Locality.—Emerald Lake SR, UWBM loc. C0241.

Age.—Late Arikareean.

Range of most closely related species.—Late-early Arikareean: Upper *Meniscomys* Concurrent-range Zone, Deep River Formation, Meagher County, Montana (*N. blacki* Rensberger, 1981).

Referred specimens.—AMNH 89725, mandible with P_4–M_3. AMNH 89800, maxilla with P^4–M^3.

Discussion.—These specimens will be described by M. C. McKenna, who generously provided casts for my inspection. Rensberger (1981), on the basis of the illustrated jaw (Love et al., 1976), referred the form to *Niglarodon* and noted a possible affinity to *N. blacki.*

Family Castoridae Gray, 1821

Genus ***Monosaulax*** Stirton, 1935

Monosaulax, cf. ***M. curtus*** (Matthew and Cook), 1909

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of similar species.—Figure 15.

Referred specimens.—P_4, KUVP 17484. P^4, KUVP 17483.

Measurements.—P_4, AP = 3.8 mm, T = 3.0 mm on occlusal surface, AP = 4.0 mm, T = 3.1 mm at base of crown. P^4, AP = 3.0 mm, T = 3.0 mm on occlusal surface, AP = 3.3 mm, T = 3.3 mm at base of crown.

Description and comparison.—In occlusal pattern, the premolars resemble similarly worn specimens of *Monosaulax pansus* (UCMP 31449) and *M. curtus* (type, AMNH 13871) illustrated by Stirton (1935). The teeth from Jackson Hole, which are too small for assignment to pre-Barstovian species or *M. pansus,* approximate those of *M. curtus, M.* near *curtus, M. complexus, M. typicus,* and *M. progressus* in size. Premolars are not known for *M. complexus. M. typicus and M. progressus* (Shotwell, 1968) differ in possessing a hypoflexus and paraflexus that overlap near the midline of P^4 in occlusal view. These two structures touch but do not overlap in *M.* near *curtus* from Anceney (Sutton, 1977; Dorr, 1956) and the Jackson Hole material. *M. progressus* further differs in the prominent anterior stylid on P_4 and anterolingual groove on P^4, both of which are absent in the premolars from Jackson Hole.

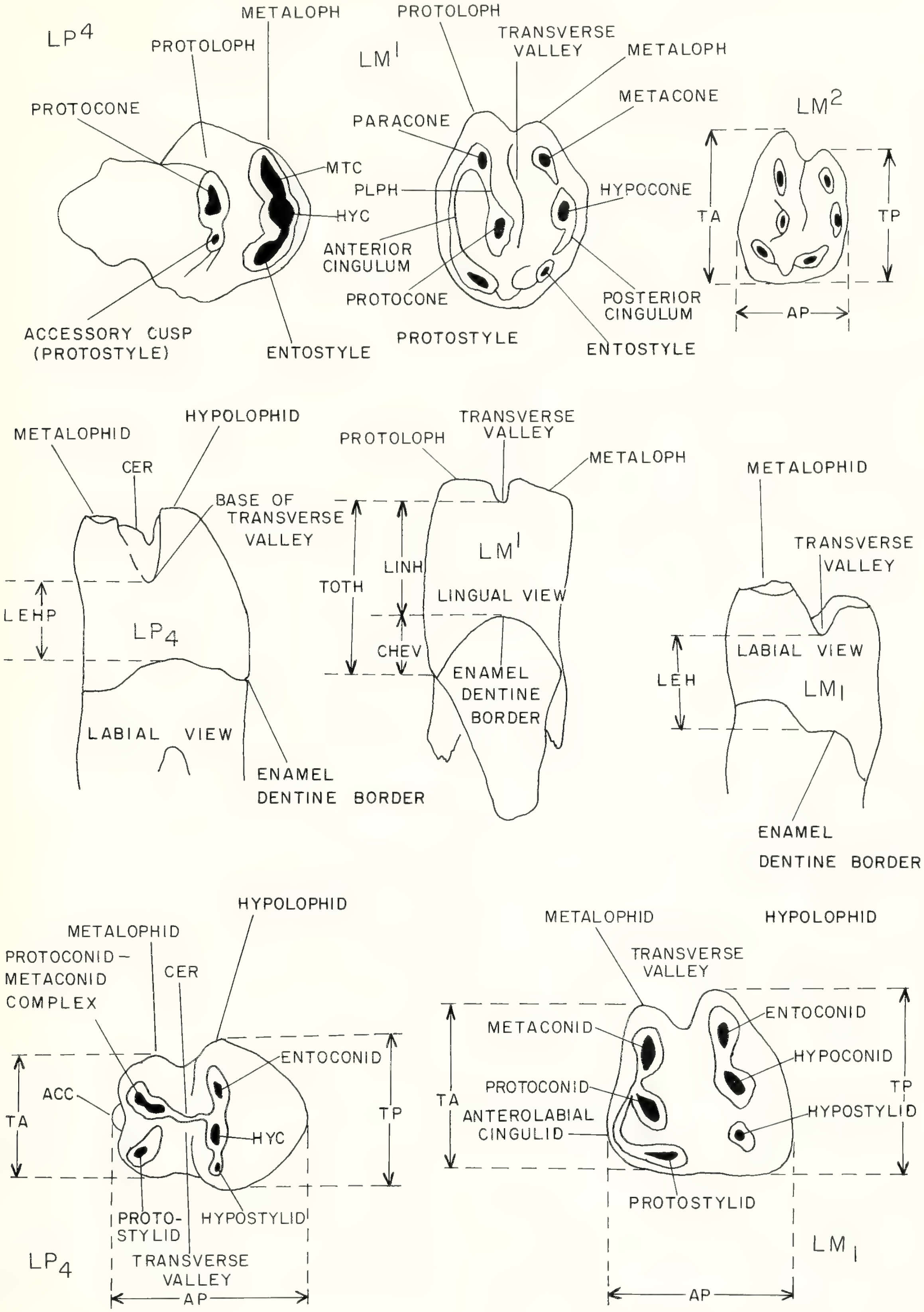
Discussion.—The teeth from Jackson Hole provide the third record of *Monosaulax* from the northern Rocky Mountains. The presence of different wear stages and different teeth complicate comparison to fossils from Anceney (*M.* near *curtus*) and Gallatin County, Montana (*M. complexus*), but beavers from all three localities are smaller than is normal for *M. pansus.* The material from Jackson Hole cannot be differentiated from the Great Plains species *M. curtus,* but because only 2 worn specimens comprise the sample referral is tentative. Stout, on the basis of his unpublished studies, believed "*Monosaulax curtus*" to be the junior synonym of "*Eucastor curtus,*" specimens of which he tentatively identified from the Fort Randall Formation of Nebraska (in Skinner and Taylor, 1967:47–49). Here I follow the majority opinion in considering *Monosaulax* a valid name, while recognizing that the relationship between *Monosaulax* and *Eucastor* deserves more detailed study.

Superfamily Geomyoidea Weber, 1904

Teeth of geomyoid rodents form the Colter Formation share the basic pattern shown in Fig. 16. Criteria listed in Fig. 17 serve to separate the genera.

→

Fig. 16.—Dental morphology, terminology, and definition of measurements in geomyoids. Abbreviations—MTC, metacone. HYC, hypocone. PLPH, protolophule. TA, greatest transverse width across anterior half of tooth. TP, greatest transverse width across posterior half of tooth. T, = TA or TP, whichever is greater. AP, longest anteroposterior dimension of tooth (transverse measurements are taken perpendicular to AP). CER, central enamel ridge (in some taxa, a central enamel pit occurs in place of the CER). TOTH, total crown height. LINH, lingual crown height. CHEV, height of enamel chevron. LEH, labial enamel height of lower molar. LEHP, Labial enamel height of lower premolar.


LP4
PROTOLOPH
METALOPH
PROTOCONE
MTC
HYC
ACCESSORY CUSP (PROTOSTYLE)
ENTOSTYLE
LM1
PROTOLOPH
TRANSVERSE VALLEY
METALOPH
METACONE
PARACONE
PLPH
HYPOCONE
ANTERIOR CINGULUM
PROTOCONE
POSTERIOR CINGULUM
PROTOSTYLE
ENTOSTYLE
LM2
TA
TP
AP
METALOPHID
HYPOLOPHID
CER
BASE OF TRANSVERSE VALLEY
LEHP
LP4
LABIAL VIEW
ENAMEL DENTINE BORDER
PROTOLOPH
TRANSVERSE VALLEY
METALOPH
TOTH
LINH
LM1
LINGUAL VIEW
CHEV
ENAMEL DENTINE BORDER
METALOPHID
TRANSVERSE VALLEY
LABIAL VIEW
LEH
LM1
ENAMEL DENTINE BORDER
HYPOLOPHID
METALOPHID
PROTOCONID—METACONID COMPLEX
CER
ENTOCONID
ACC
TA
HYC
TP
PROTO-STYLID
HYPOSTYLID
TRANSVERSE VALLEY
AP
LP4
METALOPHID
HYPOLOPHID
TRANSVERSE VALLEY
ENTOCONID
METACONID
HYPOCONID
PROTOCONID
TA
TP
ANTEROLABIAL CINGULID
HYPOSTYLID
PROTOSTYLID
LM1
AP

DISTINGUISHING FEATURES BETWEEN GENERA OF GEOMYOIDS FROM THE COLTER FORMATION

CHARACTER	SIZE						
Width (T) of M^{1-2}_{1-2}	Large 1.7 to 2.1 mm *Lignimus* *Mojavemys*		Medium 1.4 to 1.7 mm *Diprionomys* *Peridiomys*		Small 0.8 to 1.5 mm *Proheteromys, Perognathus, Cupidinimus*		
	OCCLUSAL PATTERN						
Molar Lophids	*Lignimus* *(1)* V-SHAPED JOIN CENTRAL	*Mojavemys* *(2)* STRAIGHT JOIN LABIAL	*Diprionomys* *(3)* = 2	*Peridiomys* *(4)* = 2	*Proheteromys* *(5)*	*Perognathus* *(6)* = 2	*Cupidinimus* *(7)* = 2
P^4 Protoloph	JOIN METALOPH CENTRAL	JOIN METALOPH LINGUAL	= 2		= 2	= 1	= 1
P_4	CENTRAL PIT FORMS WITH WEAR	LOPHIDS JOIN CENTRAL	LOPHIDS JOIN FIRST LABIAL CENTRAL PIT FORMS				= 2
Enamel Thickness	THICK	= 1	THICK EXCEPT POSTERIOR PART OF M^{1-2}	THIN	= 4	= 4	= 4
	HYPSODONTY						
Lower Molars LEH	LOW CROWN 0.6 to 0.7 mm	MEDIUM-HIGH 0.6 to 1.0 mm	HIGH 0.7 mm	LOW 0.5 to 0.6 mm	LOW	LOW 0.5 mm	MEDIUM 0.6 to 0.8 mm
Upper Molars LINH		1.0 to 1.1 mm unworn LINH/T = 0.59 to 0.65	0.8 to 1.0 mm worn	0.8 mm unworn LINH/T = 0.50			0.6 to 0.8 mm unworn LINH/T = 0.46 to 0.62
Upper Molar Roots		LABIAL FUSION 0.5 to 0.6 mm ABOVE CROWN	LABIAL FUSION 0.6 to 0.7 mm	LABIAL FUSION 0.2 mm			LABIAL FUSION 0.3 to 0.5 mm
Basal Bulge of Crown Wall	SLIGHT	= 1	STRAIGHT	STRAIGHT TO VERY SLIGHT	OBVIOUS	= 5	= 3

Fig. 17.—Morphologic characters that differentiate genera of geomyoid rodents that occur in the Colter Formation. The symbols =1, =2, =3, etc. indicate that the character is the same as in taxon (1) *Lignimus,* (2) *Mojavemys,* (3) *Diprionomys,* etc.

Family Heteromyidae Allen and Chapman, 1893
Subfamily Perognathinae Coues, 1875
Genus **Perognathus** Wied-Neuwied, 1839

Perognathus furlongi Gazin, 1930

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

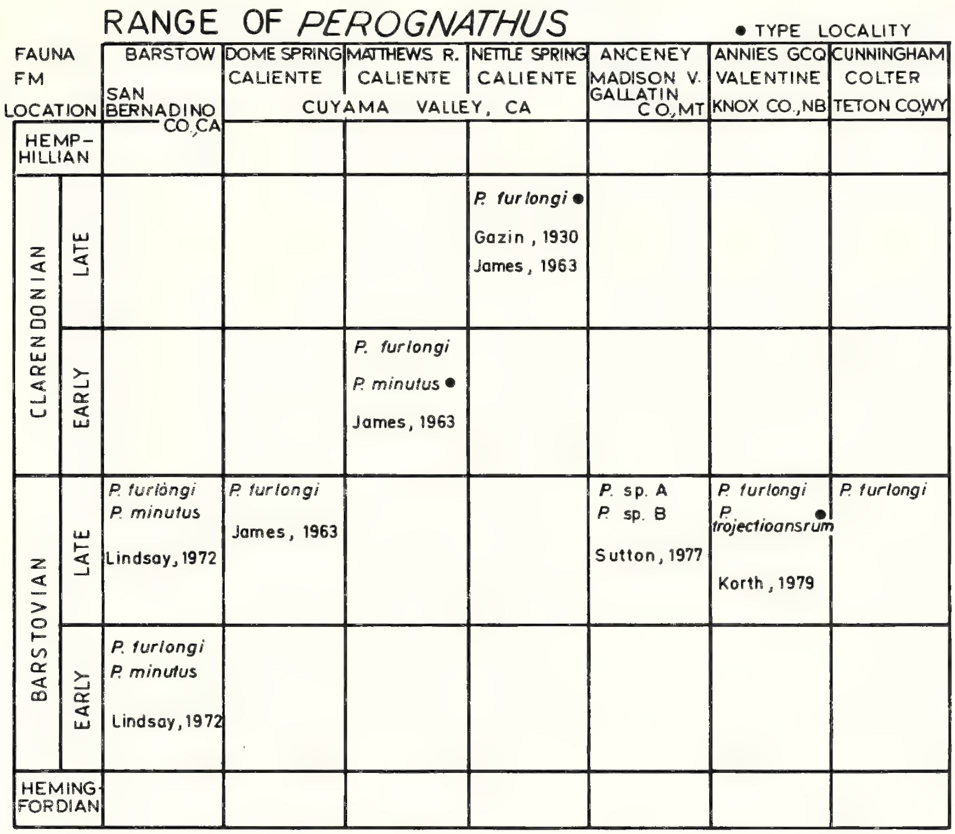
Age.—Late Barstovian.

Range of middle Miocene species.—Fig. 18.

Referred specimens.—M_1, KUVP 17810, UWBM 62612, 62697. P^4, KUVP 17808, 17801, UWBM 62789. UWBM 62612 from UWBM loc. C0237, others from UWBM loc. C0236.

Measurements.—Table 7 and Korth (1979), Lindsay (1972), James (1963), Gazin (1930), Barnosky (1983).

Description and comparison.—The brachyodont cheek teeth from Jackson Hole show the typical pattern for *Perognathus* (Fig. 16), which has been described in detail by Wood (1935), James (1963), and Lindsay (1972) among others. Crowns have bulbous bases, and the loph(ids) of the premolars join centrally. Of known Barstovian and Clarendonian species, teeth of *P. minutus* and *P. trojectioansrum* are smaller than those from Jackson Hole. Material from Jackson Hole falls within the known size range for *P. furlongi* and the Anceney *P.* sp. A (Sutton,



RANGE OF *PEROGNATHUS* ● TYPE LOCALITY

FAUNA FM LOCATION		BARSTOW SAN BERNADINO CO, CA	DOME SPRING CALIENTE CUYAMA VALLEY, CA	MATTHEWS R. CALIENTE CUYAMA VALLEY, CA	NETTLE SPRING CALIENTE CUYAMA VALLEY, CA	ANCENEY MADISON V. GALLATIN CO, MT	ANNIES GCQ VALENTINE KNOX CO., NB	CUNNINGHAM COLTER TETON CO, WY
HEMPHILLIAN								
CLARENDONIAN	LATE				*P. furlongi* ● Gazin, 1930 James, 1963			
	EARLY			*P. furlongi* *P. minutus* ● James, 1963				
BARSTOVIAN	LATE	*P. furlongi* *P. minutus* Lindsay, 1972	*P. furlongi* James, 1963			*P.* sp. A *P.* sp. B Sutton, 1977	*P. furlongi* *P. trojectioansrum* ● Korth, 1979	*P. furlongi*
	EARLY	*P. furlongi* *P. minutus* Lindsay, 1972						
HEMINGFORDIAN								

Fig. 18.—Geographic and stratigraphic range of Barstovian and Clarendonian species of *Perognathus*.

1977). As commonly happens in *P. furlongi*, stylids of M_1 join with wear in the Jackson Hole material. Lower molars from Anceney more commonly show central union of the lophids (Sutton, 1977:71).

Subfamily Dipodomyinae Coues, 1875
Genus *Cupidinimus* Wood, 1935

***Cupidinimus* sp.**
Plate IV A–L

Proheteromys Sutton and Black (1972), in part.

Localities.—North Pilgrim 2, UWBM loc. C0237, Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Early Barstovian: Barstow Formation, San Bernardino County, California (*C. halli* Wood, 1936; *C.* "*nebraskensis*") (Lindsay, 1972). Late Barstovian: Barstow Formation (*C. halli* Wood, 1936; *C. halli* Lindsay, 1972). Madison Valley Formation, Gallatin County, Montana (*C. madisonensis* Dorr, 1956). Valentine Formation, Cherry, Brown, and Knox Counties, Nebraska (*C. nebraskensis* Wood, 1935) (Klingener, 1968; Korth, 1979). Wood Mountain Formation, Saskatchewan (*C. kleinfelderi* Storer, 1975; *C. saskatchewanensis* Storer, 1975). Early Clarendonian: Esmeralda Formation, Esmeralda County, Nevada (*C. tertius* Wood, 1935; *C. quartus* Wood, 1935). Avawatz Formation, San Bernadino County, California (*C.* "cf. *C. tertius*") (Wilson, 1939). Late Clarendonian: Caliente Formation, Ventura County, California (*C. cuyamensis* Wood, 1937) (James, 1963). Hemphillian: Bidahochi Formation, Navajo County, Arizona (*C. bidahochiensis* Baskin, 1979).

Referred specimens.—From UWBM loc. C0236, P_4, UWBM 62790–62793, 62798. M_1, UWBM 62800, 62801, 62803, 62807, KUVP 17494. M_2, UWBM 62809, 62813, KUVP 17805, 17806, 17809. M_3, UWBM 62805, KUVP 17811, 17812, 17814. P^4, UWBM 62787, 62788, 62794–62796, KUVP 17500, 17802. M^1, UWBM 62799, 62806, 62810, 62812, KUVP 17804. M^2, UWBM 62802, 62811, KUVP 17803, 17813, 17815.

From UWBM loc. C0237, P_4, UWBM 62609. M_1, UWBM 62601, 62610. M_2, UWBM 62602, 62603. M_3, UWBM 62614.

Table 7.—*Dental measurements,* Perognathus furlongi, *Colter Formation.*

Tooth	Specimen	AP	T	Locality
P^4	UWBM 62789	1.0	1.1	Cunningham Hill
P^4	KUVP 17801	1.1	1.2	Cunningham Hill
P^4	KUVP 17808	1.0	1.1	Cunningham Hill
M_1	UWBM 62612	1.0	1.1	North Pilgrim 2
M_1	UWBM 62797	0.9	1.1	Cunningham Hill
M_1	KUVP 17810	1.1	1.1	Cunningham Hill

Table 8.—*Dental measurements,* Cupidinimus, *Colter Formation.*

Tooth	Statistic	AP	T	TA	TP
P_4	Mean	1.12	—	0.83	1.01
	SD	0.075	—	0.042	0.058
	OR	1.0–1.2	—	0.8–0.9	0.9–1.1
	N	6	—	6	6
M_1	Mean	1.12	—	1.24	1.29
	SD	0.065	—	0.079	0.077
	OR	1.0–1.2	—	1.1–1.4	1.2–1.4
	N	8	—	8	8
M_2	Mean	1.00	—	1.18	1.11
	SD	0.079	—	0.057	0.102
	OR	0.9–1.1	—	1.1–1.3	0.9–1.2
	N	5	—	5	5
M_3	Mean	0.73	—	1.0	0.8
	SD	0.058		0.100	0.100
	OR	0.7–0.8	—	0.9–1.1	0.7–0.9
	N	3	—	3	3
P^4	Mean	1.21	1.31	—	—
	SD	0.069	0.099	—	—
	OR	1.1–1.3	1.2–1.4	—	—
	N	7	10	—	—
M^1	Mean	0.94	1.37	—	—
	SD	0.079	0.075	—	—
	OR	0.9–1.1	1.3–1.5	—	—
	N	7	7	—	—
M^2	Mean	0.92	1.26	—	—
	SD	0.044	0.089	—	—
	OR	0.9–1.0	1.2–1.4	—	—
	N	5	5	—	—

P^4, UWBM 62594–62597, 62608. M^1, UWBM 62598, 62599. M^2, UWBM 62604, 62605.

Measurements.—Table 8 and Barnosky (1983, 1986).

Discussion.—Because of the abundance and complexity of the material, taxonomy of *Cupidinimus* is treated in a separate report (Barnosky, 1986). The Jackson Hole species is more advanced than *C. nebraskensis, C. halli, C. madisonensis, C. eurekensis,* and *C. saskatchawanensis* in its larger size, but is smaller than post-Barstovian forms. It resembles Barstovian species in having a narrow M_2 relative to length, contrasting with the wide M_2 of post-Barstovian species. The teeth from Jackson Hole resemble those of Barstovian species in crown height. Teeth in Clarendonian species have higher crowns (Barnosky, 1986).

Subfamily Heteromyinae Coues, 1875
Genus *Peridiomys* Matthew, 1924
Plate IV M–P

***Peridiomys*, species indeterminate**

Proheteromys Sutton and Black (1972), in part.

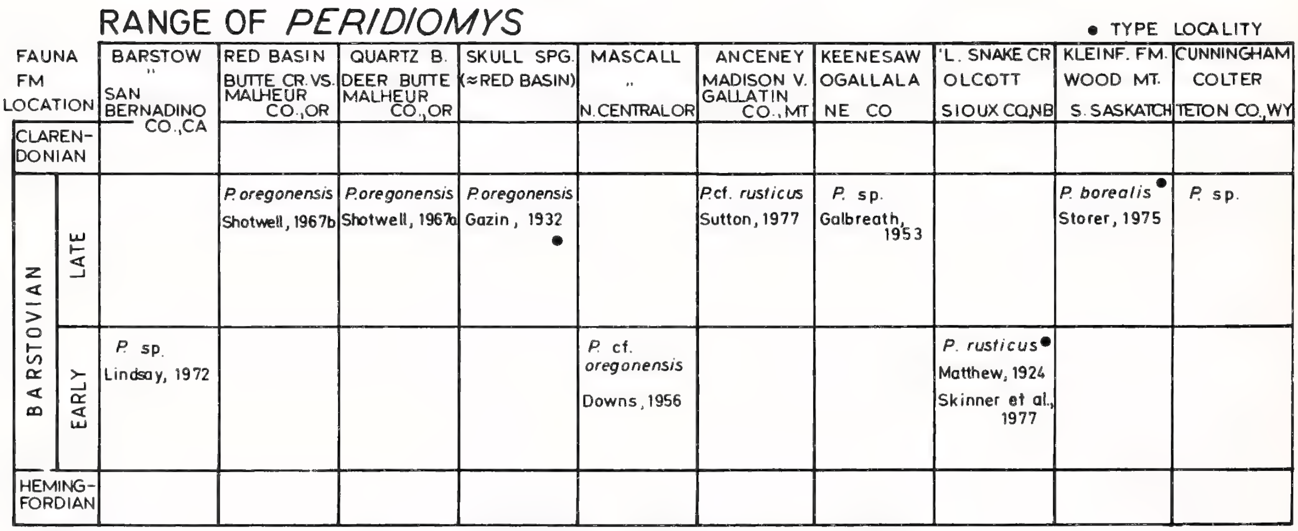
Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Fig. 19.

Referred specimens.—M_1 or M_2, UWBM 62676, 62664, KUVP 17496. M_3, UWBM 62683. M^1 or M^2, UWBM 62638, 62648. KUVP 17496 from Cunningham Hill, others from North Pilgrim 2.

Measurements.—Table 9 and Wood (1935), Shotwell (1967*b*), Downs (1956), Barnosky (1983).



RANGE OF *PERIDIOMYS*

● TYPE LOCALITY

		BARSTOW	RED BASIN	QUARTZ B.	SKULL SPG.	MASCALL	ANCENEY	KEENESAW	'L. SNAKE CR	KLEINF. FM.	CUNNINGHAM
FAUNA FM LOCATION		″ SAN BERNADINO CO.,CA	BUTTE CR. VS. MALHEUR CO.,OR	DEER BUTTE MALHEUR CO.,OR	(≈RED BASIN)	″ N. CENTRAL OR	MADISON V. GALLATIN CO., MT	OGALLALA NE CO	OLCOTT SIOUX CO.,NB	WOOD MT. S. SASKATCH	COLTER TETON CO.,WY
CLARENDONIAN											
BARSTOVIAN	LATE		*P. oregonensis* Shotwell, 1967b	*P. oregonensis* Shotwell, 1967a	*P. oregonensis* Gazin, 1932 ●		*P. cf. rusticus* Sutton, 1977	*P.* sp. Galbreath, 1953		*P. borealis* ● Storer, 1975	*P.* sp.
	EARLY	*P.* sp. Lindsay, 1972				*P.* cf. *oregonensis* Downs, 1956			*P. rusticus* ● Matthew, 1924 Skinner et al., 1977		
HEMINGFORDIAN											

Fig. 19.—Geographic and stratigraphic range of *Peridiomys.*

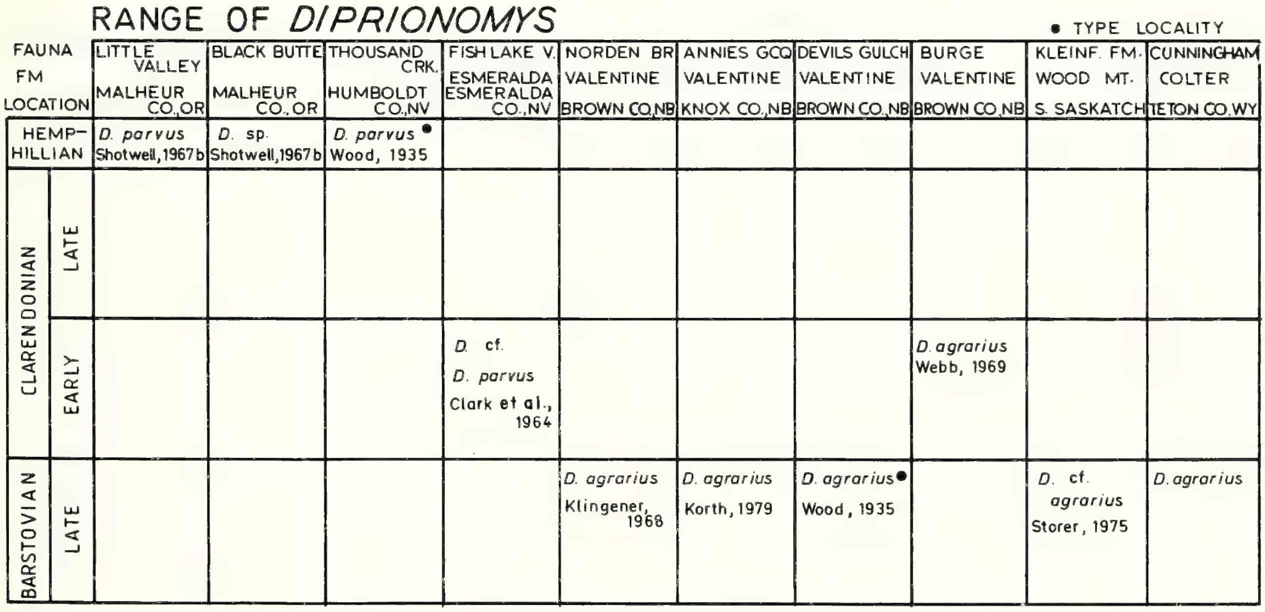
Table 9.—*Dental measurements,* Peridiomys, *Colter Formation.*

Tooth	Specimen	AP	TA	TP	AP/T	Locality
			Lower Teeth			
$M_{1 \text{ or } 2}$	UWBM 62676	1.2	1.4	1.3	0.86	North Pilgrim 2
$M_{1 \text{ or } 2}$	UWBM 62664	1.2	1.4	1.4	0.86	North Pilgrim 2
$M_{1 \text{ or } 2}$	KUVP 17496	1.3	1.4	1.4	0.93	Cunningham Hill
M_3	UWBM 62683	1.0	1.1	1.0	0.91	North Pilgrim 2
			Upper Teeth			
$M^{1 \text{ or } 2}$	UWBM 62638	1.1	1.6	1.5	0.69	North Pilgrim 2
$M^{1 \text{ or } 2}$	UWBM 62648	1.0	1.3	1.2	0.77	North Pilgrim 2

Description and comparison.—Lower molars of *Peridiomys* from Jackson Hole (Pl. IV M, N) are smaller than those of *P. rusticus* and *P.* cf. *P. rusticus* (Fig. 19), in which measurement T exceeds 1.7 mm. The sizes of the Jackson Hole teeth fall within the range for *P. oregonensis* and probably within that for *P. borealis.* The following UWBM and KUVP specimens from Jackson Hole are nearly identical to previously described and figured teeth of *P. oregonensis* from Red Basin: UWBM 62664 to UO 22877 (Shotwell, 1967*b*:fig. 9a), and KUVP 17496 to UO 24207 (Shotwell, 1967*b*:fig. 9c). M_3 has two roots, with the anterior one the most prominent.

M^1–M^2 from Jackson Hole most closely resemble specimens of *P.* cf. *P. oregonensis* from the Mascall fauna in size. The type of *P. oregonensis* is slightly larger. In occlusal pattern, an unworn specimen from Jackson Hole (Pl. IV O, P) also resembles an M^1 of *P.* cf. *P. rusticus* from Anceney (CMNH 27908). The protocone protrudes just posterior to the protostyle and paracone, which connect by a prominent anterior cingulum. On the metaloph, slight posteriad offset of the hypocone causes minor curvature of the loph and no posterior cingulum is present. With wear, the lophs join lingually to form a horseshoe shape, and in extreme wear a uniformly wide band of enamel surrounds a single dentine field. Three roots are well developed, with the labial two beginning to bifurcate 0.2 mm below the enamel-dentine border.

Discussion.—The molars of *Peridiomys* from Jackson Hole are too small to be assigned to *P. rusticus* or *P.* cf. *P. rusticus.* The size of the teeth from Jackson Hole resembles that in *P. oregonensis, P.* cf. *P. oregonensis,* and *P. borealis.* In occlusal pattern, teeth from Jackson Hole are nearly identical


RANGE OF *DIPRIONOMYS*
● TYPE LOCALITY

FAUNA FM LOCATION		LITTLE VALLEY MALHEUR CO.,OR	BLACK BUTTE MALHEUR CO.,OR	THOUSAND CRK. HUMBOLDT CO.,NV	FISH LAKE V. ESMERALDA ESMERALDA CO.,NV	NORDEN BR VALENTINE BROWN CO.,NB	ANNIES GCQ VALENTINE KNOX CO.,NB	DEVILS GULCH VALENTINE BROWN CO.,NB	BURGE VALENTINE BROWN CO.,NB	KLEINF. FM. WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO.,WY
HEMPHILLIAN		*D. parvus* Shotwell, 1967b	*D.* sp. Shotwell, 1967b	*D. parvus* ● Wood, 1935							
CLARENDONIAN	LATE										
	EARLY				*D.* cf. *D. parvus* Clark et al., 1964				*D. agrarius* Webb, 1969		
BARSTOVIAN	LATE					*D. agrarius* Klingener, 1968	*D. agrarius* Korth, 1979	*D. agrarius* ● Wood, 1935		*D.* cf. *agrarius* Storer, 1975	*D. agrarius*

Fig. 20.—Geographic and stratigraphic range of *Diprionomys.*

Table 10.—*Dental measurements,* Diprionomys agrarius, *Colter Formation.*

Tooth	Specimen	AP	TA	TP	AP/T	Locality
			Lower Teeth			
P_4	UWBM 62660	1.4	1.2	1.4	1.00	North Pilgrim 2
$M_{1 \text{ or } 2}$	UWBM 62671	1.4	1.6	1.4	0.88	North Pilgrim 2
M_3	UWBM 62275	1.3	1.6	—	0.81	North Pilgrim 2
M_3	UWBM 62677	1.2	1.4	—	0.86	North Pilgrim 2
			Upper Teeth			
$M^{1 \text{ or } 2}$	UWBM 62626	1.3	1.7	1.5	0.76	North Pilgrim 2
$M^{1 \text{ or } 2}$	UWBM 62630	1.0	1.6	1.3	0.63	North Pilgrim 2
$M^{1 \text{ or } 2}$	UWBM 62631	1.3	1.6	1.4	0.81	Cunningham Hill
$M^{1 \text{ or } 2}$	UWBM 62769	1.2	1.5	1.4	0.80	Cunningham Hill
$M^{1 \text{ or } 2}$	UWBM 62772	1.2	1.5	1.4	0.80	Cunningham Hill

to those of *P. oregonensis.* Teeth in similar wear stages have not been reported for other species, thus precluding species identification.

Genus *Diprionomys* Kellogg, 1910

Diprionomys agrarius Wood, 1935
Plate II D–H

Proheteromys Sutton and Black (1972), in part.

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Fig. 20.

Referred specimens.—P_4, UWBM 62660. M_1 or M_2, UWBM 62671. M_3, UWBM 62675, 62677. P^4, KUVP 17499. M^1 or M^2, UWBM 62626, 62630, 62631, 62722. M^2, UWBM 62769. UWBM 62769, 62772, and KUVP 17499 from Cunningham Hill, others from North Pilgrim 2.

Measurements.—Table 10 and Wood (1935), Korth (1979), Klingener (1968), Storer (1975), Shotwell (1967*b*), Clark et al. (1964), Barnosky (1983).

Description and comparison.—The P_4 is more worn than that of the type specimen for *D. agrarius,* but similar in general morphology. At least three cusps form the metalophid, with the labial one joining the hypolophid in late wear (Pl. II F). Lingually, the metalophid barely touches the hypolophid and isolates a central basin. At a similar stage of wear, the same condition would prevail in all *Diprionomys* that I have seen. The size of the P_4 from Jackson Hole most closely approximates that of *Diprionomys agrarius* from Norden Bridge and Knox County. As in the type of *D. agrarius,* the roots fuse for at least 1 mm below the base of the crown, where they are broken off.

Like the condition in *Diprionomys agrarius,* in which four M_{1-2}'s average 1.4 mm AP, the size of lower molars from Jackson Hole exceeds that of *D. parvus,* in which lower (n = 5) and upper (n = 4) M_{1-2}'s average 1.1 mm AP (Wood, 1935; Shotwell, 1967*b*; Clark et al., 1964). Although wear has removed cusps from the Jackson Hole specimens, the general outline of the lophids in UWBM 62671 (Pl. II E) closely approximates that in the type of *D. agrarius.*

M_3's from Jackson Hole (Table 10) are not much smaller than the M_1 or $_2$. They about equal P_4 in width, as Wood (1935:179) noted for the type of *D. agrarius.* The M_3 from Knox County was found to be wider than the P_4 (Korth, 1979:302). Equally wide anterior and posterior lophids connect to a single simple root in the teeth from Jackson Hole, as Shotwell also described for *D. parvus.*

The single fragment of P^4 shows a transversely elongate but essentially single cusped photoloph that connects to the entostyle via a short ridge. Connection is much less prominent than in *D. parvus* and the protoloph is much narrower. The entostyle, which is considerably more anterior with respect to the metaloph than in *D. parvus,* nearly aligns with the protoloph. The entostyle in *D. parvus* is located well posterior of the protoloph, although it is still the most anterior cusp on the metaloph. Judging from figures in Clark et al. (1964), the entostyle in a P^4 from the Esmeralda Formation occurs farther posterior than in the Jackson Hole specimen, but farther anterior than in *D. parvus.* The width of the tooth from Jackson Hole (1.55 mm minimum) exceeds that of *D.* cf. *D. agrarius* from the Wood Mountain Formation (1.3 mm, mean of 7 specimens, OR = 1.13–1.41 mm, Storer, 1975) or *D.* cf. *D. parvus* (1.43 mm, Clark et al., 1964). It is narrower, however, than in *D. agrarius* from Knox County (1.78 mm, mean of 4 specimens, OR = 1.62–

RANGE OF *LIGNIMUS*

● TYPE LOCALITY

FAUNA		NIOBRARA R.	NORDEN BR	ANNIES GCQ	BURGE	WAKEENEY	KLEINF. FM.	CUNNINGHAM
FM		VALENTINE	VALENTINE	VALENTINE	VALENTINE	OGALLALA	WOOD MT.	COLTER
LOCATION		CHERRY CO.,NB	BROWN CO.,NB	KNOX CO.,NB	BROWN CO.,NB	TREGO CO.,KS	S. SASKATCH	TETON CO.,WY
HEMPHILLIAN								
CLARENDONIAN	LATE					*L. hibbardi* ● Storer, 1973		
	EARLY				*L.* sp. Storer, 1973			
BARSTOVIAN	LATE	*L.* sp. Storer, 1973	*L.* sp. *L.* cf. *montis* Storer, 1973	*L.* cf. *hibbardi* Korth, 1979			*L. montis* ● Storer, 1973 1975	*L. transversus* ● new species

Fig. 21.—Geographic and stratigraphic range of *Lignimus.*

1.87, Korth, 1979), and falls near the average for *D. parvus* from Little Valley (1.49 mm, mean of 5 specimens, OR = 1.18–1.74, Shotwell, 1967*b*).

Upper molars were hitherto unknown for *D. agrarius.* One Jackson Hole M^2 is virtually unworn and shows that three transversely aligned cusps compose each of the lophs. The lophs lack anterior and posterior cingula. The protocone is anteroposteriorly compressed, flattened anteriorly, and aligns almost exactly with the protostyle and paracone. The protocone nearly touches the protostyle, but a notch separates it from the paracone. On the metaloph, the hypocone occurs slightly posterior to the entostyle and metacone, and a ridge of enamel connects all three cusps. *D. parvus* from Little Valley (UO 26014) differs in the more pronounced cingula, which would be expected if the tooth is an M^1 rather than M^2.

Worn M^1–M^2 from Jackson Hole (Pl. II D) are horseshoe shaped because the protoloph and metaloph fuse lingually, as also occurs in *D. parvus.* Unlike *D. parvus,* lophs in the Jackson Hole specimens do not join labially to isolate a central lake. In upper molars from Jackson Hole, enamel on the most posterior band is only about half as thick as on the rest of the occlusal surface (Pl. II D). This contrasts with two illustrations of *D. parvus* where enamel slightly thins anteriorly (UO 26004) or is of about equal width (UO 26024) throughout. A third tooth of *D. parvus* shows posterior thinning of the enamel (UO 26022) (Shotwell, 1967*a*). In labial view, roots on the Jackson Hole M^1–M^2's fuse for about 0.7 mm above the crown, with the remaining unfused portion measuring about 1.0 mm. In contrast, the fused portion of the root is longer than the unfused portion in *D. parvus* (UO 26014).

Discussion.—Teeth from Jackson Hole do not differ significantly from the type of *Diprionomys agrarius* or the Norden Bridge material. Small samples suggest that individuals of *D. agrarius* from the Knox County, Nebraska, locality were probably larger but of the same species. Cheek teeth of *D. agrarius* are less hypsodont than in *D. parvus,* shown by greater fusion of roots and labial closure of the transverse valley in upper molars of *D. parvus.* Labial closure is accomplished by development of a labial enamel ridge between the two lophs. The Jackson Hole material and other *D. agrarius* also differ from *D.* cf. *D. parvus* in larger size.

Korth (1979) suggested that *D. parvus* from Little Valley and Thousand Creek (Fig. 20) represents a genus other than *Diprionomys.* Of the characters that I have seen, the configuration of P^4 may support that conclusion, but samples of the commonly variable tooth are very small. I include *D. parvus* in *Diprionomys,* while recognizing the possibility that *D. parvus* is phylogenetically more distant from *D. agrarius* than is *D.* cf. *D. parvus,* as Korth (1979) suggested. *D.* cf. *D. agrarius* from the Wood Mountain Formation, because of its small size, may represent a distinct species more closely related to *D. agrarius,* but more material is needed for accurate diagnosis.

Genus ***Proheteromys*** Wood, 1932

***Proheteromys,* species indeterminate**

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range.—Arikareean through Barstovian of North America.

Referred specimens.—P^4, KUVP 17807.

Discussion.—The small, worn P^4 measures 1.0 (AP) × 1.0 mm (T), is brachyodont, and shows a protoloph joined to the entostyle as is typical of *Proheteromys.* Species diagnosis is not possible.

Family Geomyidae Gill, 1872

Subfamily uncertain

Genus ***Lignimus*** Storer, 1970

Lignimus transversus, new species

Plate V

Proheteromys Sutton and Black (1972), in part.

Holotype.—UWBM 62662, right M_1 or M_2.

Hypodigm.—UWBM 62655 (P_4), 62663, 62666, 62668, 62669, 62681 (M_1 or M_2), 62686, 62687 (M_3), 62616 (P^4), 62611, 62621, 62624, 62629, 62634, 62635 (M^1 or M^2), 62644, 62645 (M^3).

Type Locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—"Transversus" referring to transversely straight anterior margin of hypolophid.

Age.—Late Barstovian.

Range of genus.—Fig. 21.

Referred specimens.—P_4, UWBM 62652, 62758. M_1 or M_2, UWBM 62782, 62785. M_3, UWBM 62779, 62781, KUVP 17495. P^4, UWBM 62760. M^1 or M^2, UWBM 62768, 62771, 62777, KUVP 17490. UWBM 62652 from type locality, others from Cunningham Hill, loc. C0236.

Measurements.—Table 11 and Storer (1973, 1975), Korth (1979), and Barnosky (1983).

Diagnosis.—Cheek teeth brachyodont, roots present, dentine tracts absent. P_4 with two cusps on metalophid (versus three or four in *L. montis*), ratio AP/T more than 1.0. M_1–M_2 with prominent anterolabial lake, V shaped lophs, ratio of AP/T ranging from about 0.76 to 0.89, hypolophid anteriorly flatter than in *L. montis.* M_3 with ratio of AP/T generally between 0.85 and 0.93, connection between metalophid and hypolophid not pronounced. P^4 with ratio AP/T less than 1.00, single cusp usual on protoloph. M^1–M^2 with relatively bulbous cusps, ratio AP/T usually between 0.70 and 0.75. Molars larger than in *L. montis,* with average AP of M_1 and M_2 = 1.46 mm (versus 1.26 mm in *L. montis*), average AP of M^1 and M^2 = 1.28 mm (versus 1.14 mm).

Description and comparison.—The cheek teeth from Jackson Hole are relatively brachyodont and lack dentine tracts (Pl. V). Teeth of *L. montis* are similar in these respects. *L.* sp. (Fig. 21) and *L.* cf. *L. hibbardi* have tracts that reach about half the height of the molar crown. In *L. hibbardi,* tracts are two-thirds as high as the crown. M_1 and M_2 of *L. transversus* (Pl. V F) and *L. montis* have roots; these teeth lack roots in *L.* cf. *L. hibbardi* and *L. hibbardi.* In P_4 of *L. transversus,* the protoconid-metaconid complex forms a single cusp that is separated from the protostylid by a slight anterior notch (Pl. V B). In contrast, at least three prominent cusps make the metalophid of *L. montis,* with the most anterior one forming a projection in the same area as the notch occurs in *L. transversus* (compare Pl. V B with fig. 75A, B in Storer, 1975). Where P_4 is known, other *Lignimus* resemble *L. montis* in this respect. The hypolophid in *L. transversus,* as in all species, is composed mainly of two transversely aligned cusps, the hypoconid and entoconid. The hypostylid in *L. transversus* is rudimentary. P_4 of *L. transversus* is slightly narrower than the single comparative specimens of *L. montis* and *L. hibbardi* (ratio AP/T = 1.0), but wider than the average of 11 teeth of *L.* cf. *L. hibbardi* (mean, ratio AP/T = 1.15) (Korth, 1979; Storer, 1973, 1975; and Table 11). P_4 of *L. transversus* is about 10% smaller than in *L. montis,* and 10%–20% smaller than in *L.* cf. *L. hibbardi* and *L. hibbardi.*

M_1–M_2 of *L. transversus* (Pl. V A, C–H) closely resemble those of *L. montis,* which Storer (1975) described in detail. The protoconid and metaconid, which are set relatively far posterior of the anterior border of the tooth, are prominent (Pl. V C). Ridges project anteromedially from the center of each cusp and meet near the center of the anterior border. They thus form a rostrally pointing V. A posterior V, formed by ridges extending off the entoconid and hypoconid, parallels the anterior one. This posterior V is considerably more prominent in worn teeth of *L. montis* than in *L. transversus.* A prominent anterolabial cingulid runs from a minute protostylid to the apex of the anterior V and, in concert with the protoconid, borders a lake that forms as the

Table 11.—*Dental measurements,* Lignimus transversus, *new species, Colter Formation.*

Tooth	Statistic* or Specimen	AP	TA	TP	AP/T	Locality
P_4	UWBM 62655	1.6	1.3	1.5	1.07	NP
	UWBM 62652	—	1.2	—	—	NP
	UWBM 62758	1.6	1.2	1.5	1.07	CH
M_1 or M_2	Mean	1.46	1.74	1.73	0.83	
	SD	0.172	0.152	0.206	0.045	NP and CH
	OR	1.3–1.7	1.6–2.0	1.5–2.1	0.76–0.89	
	N	7	5	7	6	
M_3	Mean	1.20	1.30	1.16	0.90	NP and CH
	SD	0.071	0.071	0.055	0.039	
	OR	1.1–1.3	1.2–1.4	1.1–1.2	0.85–0.93	
	N	5	5	5	5	
P^4	UWBM 62616	1.5	0.9	1.8	0.83	NP
	UWBM 62759	1.7	1.1	1.8	0.94	CH
M^1 or M^2	Mean	1.28	1.78	1.70	0.72	NP and CH
	SD	0.084	0.084	0.100	0.012	
	OR	1.2–1.4	1.7–1.9	1.6–1.8	0.71–0.74	
	N	5	5	5	5	
M^3	UWBM 62644	1.4	1.6	—	0.88	NP
	UWBM 62645	1.3	1.5	—	0.87	NP

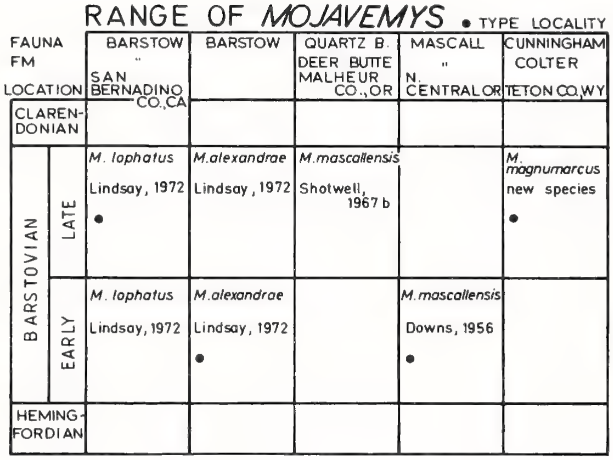
* See Barnosky (1983) for measurements of individual specimens and summary of measurements of other species.
NP North Pilgrim 2.
CH Cunningham Hill.

tooth wears (Pl. V D). Other species differ from *L. transversus* and *L. montis* in their flattening of the V's to form two straight lophs, and poor development or absence of an anterolabial enamel lake. The M_1's and M_2's in *L. montis* and *L. transversus* are relatively narrow, with the ratio of AP/T averaging 0.81 and 0.83, respectively. The ratios of AP/T are smaller, meaning wider teeth, in *L.* cf. *L. hibbardi* (OR of ratio AP/T = 0.70–0.75, n = 2) and *L. hibbardi* (OR = 0.62–0.68, n = 2).

M_3 of *L. transversus* (Pl. V I, J) resembles that in *L. montis* except for two major features. In *L. transversus,* the anterolabial enamel lake is more transient and the central connection between the metalophid and hypolophid is less pronounced. Lophids, as well as length of the tooth, are more compressed in the Burge *L.* sp. (ratio AP/T = 0.56, n = 1), *L.* cf. *L. hibbardi* (AP/T = 0.76, n = 1), and *L. hibbardi* (AP/T = 0.75–0.78, n = 2). UWBM 62779 possesses a single large root.

P^4 of *L. transversus* (Pl. V K, L, O, P), like that of all the species, is composed of a three cusped metaloph. The protoloph is composed of a single transversely ovoid cusp in all species. Some specimens of *L. montis* possess an extra cusp anterad to the protoloph. With wear, the protoloph joins the metaloph just lingual of center as in all species in which P^4 is known. Unworn cusps on the metalophid are slightly bulbous, especially the hypocone (Pl. V K). A weak posterior cingulum joins the hypocone to the entostyle, which is compressed transversely. Unworn P^4's of other species have not been reported. Like *L. hibbardi, L.* cf. *hibbardi,* and Cherry Co. *L.* sp., *L. transversus* has a short P^4 in which the ratio $AP/T < 1.00$. *L. montis* and the Norden Bridge *L.* sp. have a longer P^4 in which the ratio $AP/T \geq 1.05$. *L. transversus* resembles *L. montis* in lacking dentine tracts. Tracts are long in *L.* cf. *L. hibbardi, L. hibbardi,* and *L.* sp.

The M^1–M^2 of *L. transversus* (Pl. V M, N, Q. R, U, V) are nearly identical to those in *L. montis* and *L.* cf. *L. montis* in occlusal pattern. In teeth tentatively identified as M^1 (Pl. V M), the protoloph consists of a moderately bulbous paracone, protocone, and protostyle, with the protocone set slightly posterior to the other two. The anterior cingulum forms about one-third the anteroposterior length of the loph. The metaloph curves slightly because the hypocone rests posterior to the metacone and entostyle. In teeth tentatively identified as M^2 (Pl. V Q), the anterior cingulum is at maximum about one-fifth as long as the protoloph and the protocone is even with or slightly anterior to the paracone and protostyle. Wear soon obscures these differences, and eventually joins the lophs at their lingual margin. Except for a probable M^2 of *L.* cf. *L. hibbardi* (UNSM 56343), unworn M^1–M^2's of species other than *L. montis* have not been described. UNSM



RANGE OF *MOJAVEMYS* ● TYPE LOCALITY

FAUNA FM LOCATION		BARSTOW " SAN BERNADINO CO.,CA	BARSTOW	QUARTZ B. DEER BUTTE MALHEUR CO.,OR	MASCALL " N. CENTRAL OR	CUNNINGHAM COLTER TETON CO.,WY
CLARENDONIAN						
BARSTOVIAN	LATE	*M. lophatus* Lindsay, 1972 ●	*M. alexandrae* Lindsay, 1972	*M. mascallensis* Shotwell, 1967 b		*M. magnumarcus* new species ●
	EARLY	*M. lophatus* Lindsay, 1972	*M. alexandrae* Lindsay, 1972 ●		*M. mascallensis* Downs, 1956 ●	
HEMINGFORDIAN						

Fig. 22.—Geographic and stratigraphic range of *Mojavemys.*

56343 and slightly worn specimens of *Lignimus* sp. and *L.* cf. *L. hibbardi,* however, suggest that the cusps are transversely more flattened and anterior cingula less pronounced than in *L. transversus.* M^1–M^2 of *L. transversus* are slightly longer than in *L.* cf. *L. hibbardi* (average ratio AP/T = 0.66, OR = 0.60–0.71, n = 5), but on the average slightly shorter than in *L. montis* (average AP/T = 0.76, OR = 0.69–0.87, n = 13), *L.* cf. *L. montis* (average AP/T = 0.80, n = 4), and possibly *L. hibbardi* (average AP/T = 0.74, OR = 0.70–0.78, n = 2) (Table 11).

Two M^3's (Pl. V S, T) of *L. transversus* are known but are too worn for meaningful comparison. The lophs join lingually and after extreme wear enclose a central lake. Like all molars of *L. transversus,* M^3's are from 10%–30% larger than in *L. montis.*

Discussion.—The main evolutionary trends in *Lignimus* seem to be (1) straightening of the V shaped lophids in M_1–M_2, (2) compression of the cheek teeth anteroposteriorly, (3) increasing hypsodonty, and (4) development of dentine tracts. In all of these charaters, *L. transversus* resembles the most primitive species, *L. montis,* most closely. Less prominent V's on the hypolophids suggest that *L. transversus* is slightly more advanced than *L. montis* and morphologically closer to the stock that gave rise to later species of *Lignimus.*

Table 12.—*Dental measurements,* Mojavemys magnumarcus, *new species, Colter Formation.*

Tooth	Statistic* or Specimen	AP	TA	TP	AP/T	Locality
P_4	UWBM 62661	1.7	1.1	1.6	1.06	NP
	UWBM 62765	1.6	1.0	1.2	1.33	CH
M_1	Mean	1.57	1.82	1.78	0.85	
	SD	0.137	0.160	0.098	0.024	NP and CH
	OR	1.5–1.8	1.7–2.1	1.7–1.9	0.82–0.88	
	N	6	6	6	6	
M_2	UWBM 62665	—	1.9	—	—	NP
	UWBM 62766	1.4	1.8	1.7	0.78	CH
	UWBM 62783	1.4	1.8	1.8	0.78	CH
	KUVP 17491	1.4	1.7	1.7	0.82	CH
M_3	Mean	1.22	1.40	1.10	0.88	NP and CH
	SD	0.103	0.149	0.156	0.095	
	OR	1.1–1.4	1.2–1.7	0.9–1.4	0.73–1.08	
	N	10	10	10	10	
P^4	UWBM 62617	1.7	—	1.8	0.94	NP
	UWBM 62760	—	—	1.8[a]	—	CH
	UWBM 62776	—	—	1.9[a]	—	CH
	UWBM 62778	—	—	1.9	—	CH
M^1 or M^2	Mean	1.43	1.81	1.70	0.79	NP
	SD	0.052	0.146	0.141	0.060	
	OR	1.4–1.5	1.7–2.1	1.5–1.9	0.71–0.88	
	N	6	7	6	6	
M^3	UWBM 62646	1.1	1.4†	—	0.79	NP
	UWBM 62647	1.1	1.3†	—	0.85	NP
	KUVP 17498	1.2	1.6†	—	0.75	NP

* See Barnosky (1983) for measurements of individual specimens and summary of measurements of other species.
† Measurement T.
NP North Pilgrim 2.
CH Cunningham Hill.
[a] approximately.

Genus *Mojavemys* Lindsay, 1972

Mojavemys magnumarcus, new species

Plate VI

Proheteromys Sutton and Black (1972) in part.

Holotype.—UWBM 62641, M^1 or M^2.

Hypodigm.—UWBM 62667, 62665 (M_2) from type locality.

Type locality.—North Pilgrim 2, UWBM loc. C0237.

Etymology.—Magna (large), arcus (arch) refers to large size and prominent, arch-shaped basal chevron of upper molars.

Age.—Late Barstovian.

Range of genus.—Fig. 22.

Referred specimens.—From UWBM loc. C0237, P_4, UWBM 62661. M_1, UWBM 62673. M_3, UWBM 62678, 62679, 62680, 62682, 62684, 62689, 62690, 62691. P^4, UWBM 62617. M^1 or M^2, UWBM 62622, 62623, 62627, 62636, 62637, 62643, 62649. M^3, UWBM 62646, 62647.

From UWBM loc. C0236, P_4, UWBM 62765. M_1, UWBM 62770, 62780, 62784, 62786. M_2, UWBM 62783, 62766, KUVP 17491. M_3, UWBM 62773, 62775, KUVP 17493. P^4, UWBM 62759, 62776, 62778. M^3, UWBM 62767, KUVP 17498.

Measurements.—Table 12 and Lindsay (1972), Downs (1956), Shotwell (1967*a*), Barnosky (1983).

Diagnosis.—P_4, M_1, M_2, M^1, M^2, M^3 from 10%–30% larger than in *M. lophatus* or *M. mascallensis.* M_2 with transversely elongate metaconid, prominent anterolabial cingulid extending anterior to protoconid, cusps with more pronounced anteroposterior compression than in other species. M^1–M^2 with well developed enamel chevron at lingual base, ratio CHEV/T exceeding 0.30.

Description and Comparison.—Cusp morphology in P_4 of *M. magnumarcus* (Pl. VI A, C) approximates the morphology in *M. mascallensis* (UO 22740). Three cusps make the metalophid, with the middle one most anterior and very prominent. A short, anteroposteriorly oriented crest connects the metalophid and hypolophid. The hypolophid is compressed anteroposteriorly. Individual variation among the P_4's of *M. magnumarcus* is apparently marked, as in *M. lophatus* (Table 12). Wear stage accounts for only part of the variation in the ratio of AP/T for the Jackson Hole P_4's. With continued wear, the occlusal pattern in UWBM 62765 would approximate the pattern in the type specimen of *M. lophatus,* but the posterior border would bulge less than in *M. mascallensis.* In a worn P_4 of *M. magnumarcus* (UWBM 62661), the metalophid expands anteriorly more than in known specimens of *M. lophatus* or the type of *M. mascallensis* (UCMP 39094), but resembles *M. mascallensis* from the Quartz Basin (UO 22740 and LACM CIT 4002b). The posterior margin of the hypolophid, bulging more than in *M. lophatus,* approximates the condition in *M. mascallensis.* In *M. magnumarcus* one anterior root is preserved and is distinctly separated from the posterior roots. Separate anterior and posterior roots are also present in *M. mascallensis.*

The general morphology of M_1–M_2 in *Mojavemys magnumarcus* (Pl. VI B, D, E, F–M) closely follows that described by Lindsay (1972) for *M. lophatus* and by Shotwell (1967*a*) and Downs (1956) for *M. mascallensis.* The anterolabial cingulid of M_1 (Pl. VI B), as in *M. lophatus,* trends anteroposteriorly and extends only one third of the way across the metalophid. In *M. mascallensis* (UO 22736), the cingulid trends more transversely, and extends about half of the way across the metalophid. One anterior and one posterior root fuse near the base of the crown (as in Pl. VI L), but diverge widely ventrad like those in *M. lophatus.* Two anterior and two posterior roots, all separate, are present in *M. mascallensis.*

The M_2 in *M. magnumarcus* has an anterolabial cingulid that extends about half way across metalophid as in *M. alexandrae* and *M. lophatus.* The two M_2's that are nearly unworn, UWBM 62766 (Pl. VI D) and 62665, differ from unworn teeth of *M. alexandrae* and *M. lophatus* in the transversely wider, more lophate metaconid, and more pronounced anteroposterior compression of the lophs. These teeth also differ from *M. alexandrae* in having a more prominent anterior cingulid. The single anterior and single posterior root of *M. magnumarcus,* as in all species, separate distally (Pl. VI L). In the Jackson Hole specimen, as in *M. alexandrae,* the lateral sulcus on the lower teeth does not persist to the base of the crown and the enamel is thick, commonly between 0.10 and 0.15 mm.

The M_3 (Pl. VI E) contains two major anteroposteriorly compressed cusps on the metalophid, and two on the hypolophid. Both lophids are transversely straight. The rudimentary protostylid in some specimens connects to an anterolabial cingulum that extends from one third to one half way across the metalophid. The pattern is nearly identical in *M. alexandrae,* the only other species for which unworn M_3's are reported. With considerable wear, lophs join labially in *M. magnumarcus.* Two roots, one anterior and one posterior, curve markedly poste-

Table 13.—*Measurements, hypsodonty,* Mojavemys magnumarcus, *new species, and other species of genus.*

Tooth	Specimen	TOTH*	CHEV	T	LINH/T	CHEV/T	TOTH/T
			Mojavemys alexandrae				
M^2	UCMP 78156	1.4	0.5	1.9	0.74	0.26	1.00
M^2	UCMP 78157	—	0.4	1.8	—	0.22	—
			Mojavemys lophatus				
M^1	UCMP 78162	1.2	0.9	1.85	0.65	0.49	0.92
M^2	UCMP 78137	0.9	0.4	1.3	0.69	0.31	1.00
			Mojavemys magnumarcus				
$M^{1 \text{ or } 2}$	UWBM 62627	1.1	—	1.7 mx	0.65	—	—
$M^{1 \text{ or } 2}$	UWBM 62641	1.0	0.7	1.7	0.58	0.41	1.00

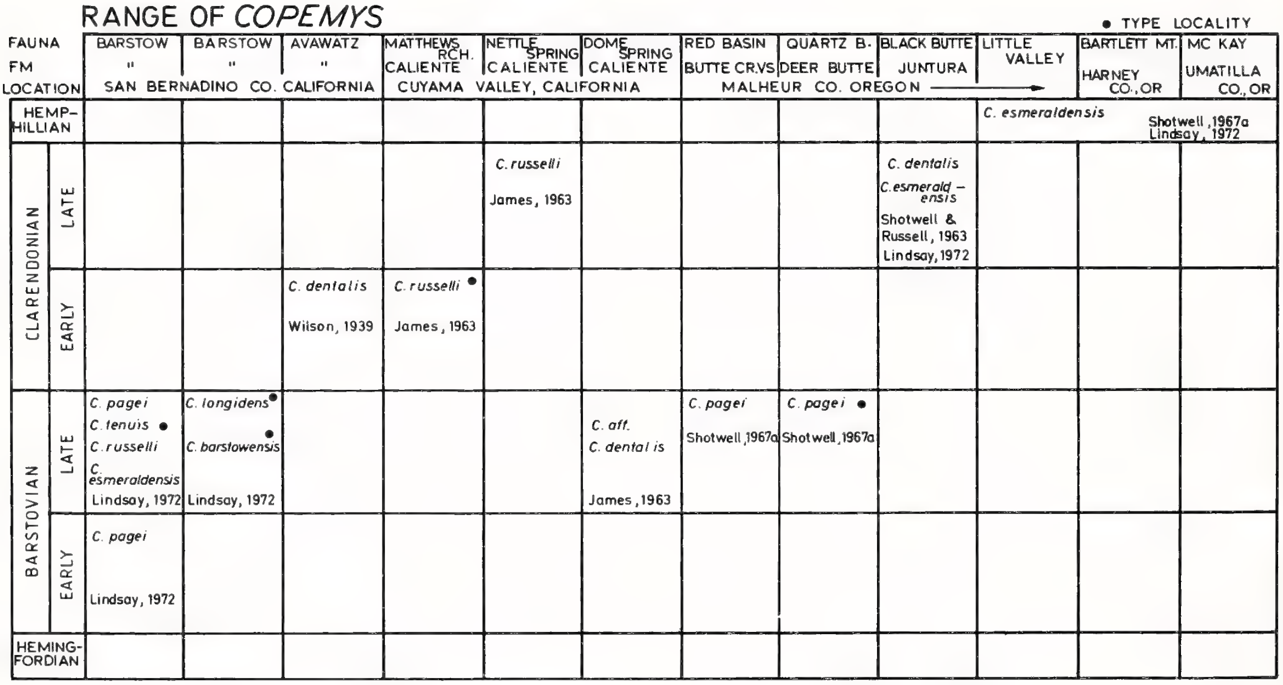
* See Fig. 16 for explanation of measurements.
mx maximum.

rad. The anterior one is rudimentary and in some specimens is fused to the posterior one.

The samples of P^4 are small for all species. In the Jackson Hole material, the protoloph is formed by a single, transversely elongate cusp (Pl. VI O, P). With wear, the protoloph joins lingually to the metaloph. The same condition prevails in all *Mojavemys.*

The M^1–M^2's from Jackson Hole (Pl. VI Q) are too worn to display details of the cusps, but resemble similarly worn specimens of *M. alexandrae* in proportions. They are anteroposteriorly shorter than teeth of *M. mascallensis* (ratio AP/T = 0.93–1.00, n = 2). Teeth of *M. magnumarcus* are on average 15% larger than those of *M. lophatus* (AP = 0.9–1.2 mm, n = 4) and 20% larger than in *M. mascallensis* (AP = 0.9–1.0 mm, n = 2). The lingual chevrons in *M. magnumarcus* (Pl. VI T) are higher than in *M. alexandrae* (Table 13, Fig. 16). The lophs in *M. magnumarcus,* like in *M. lophatus,* are slightly more compressed anteroposteriorly than in *M. alexandrae.*

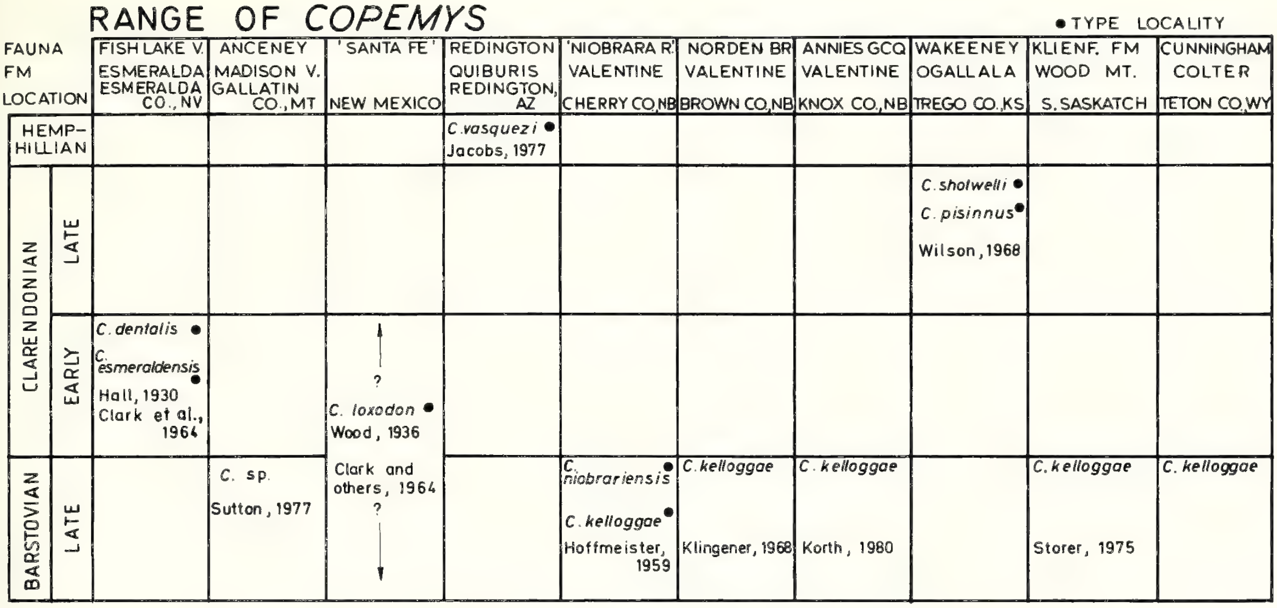
The M^3 (Pl. VI R, S), as in *M. lophatus* and *M. alexandrae,* possesses a central basin that is ringed by the protoloph and metaloph. In contrast, the central basin opens labially in *M. mascallensis.* Like the condition in *M. lophatus,* the only other taxon


RANGE OF *COPEMYS*

● TYPE LOCALITY

FAUNA		BARSTOW	BARSTOW	AVAWATZ	MATTHEWS RCH.	NETTLE SPRING	DOME SPRING	RED BASIN	QUARTZ B.	BLACK BUTTE	LITTLE VALLEY	BARTLETT MT.	MC KAY
FM		"	"	"	CALIENTE	CALIENTE	CALIENTE	BUTTE CR.VS	DEER BUTTE	JUNTURA			
LOCATION		SAN BERNADINO CO. CALIFORNIA			CUYAMA VALLEY, CALIFORNIA			MALHEUR CO. OREGON →				HARNEY CO., OR	UMATILLA CO., OR
HEMPHILLIAN											*C. esmeraldensis* Shotwell, 1967a Lindsay, 1972		
CLARENDONIAN	LATE					*C. russelli* James, 1963				*C. dentalis* *C. esmeraldensis* Shotwell & Russell, 1963 Lindsay, 1972			
	EARLY			*C. dentalis* Wilson, 1939	*C. russelli* ● James, 1963								
BARSTOVIAN	LATE	*C. pagei* *C. tenuis* ● *C. russelli* *C. esmeraldensis* Lindsay, 1972	*C. longidens* ● ● *C. barstowensis* Lindsay, 1972				*C.* aff. *C. dentalis* James, 1963	*C. pagei* Shotwell, 1967a	*C. pagei* ● Shotwell, 1967a				
	EARLY	*C. pagei* Lindsay, 1972											
HEMINGFORDIAN													

Fig. 23.—Geographic and stratigraphic range of *Copemys* in California and Oregon.



RANGE OF *COPEMYS*

● TYPE LOCALITY

FAUNA FM LOCATION		FISH LAKE V. ESMERALDA ESMERALDA CO., NV	ANCENEY MADISON V. GALLATIN CO., MT	'SANTA FE' NEW MEXICO	REDINGTON QUIBURIS REDINGTON, AZ	'NIOBRARA R.' VALENTINE CHERRY CO, NB	NORDEN BR VALENTINE BROWN CO, NB	ANNIES GCQ VALENTINE KNOX CO., NB	WAKEENEY OGALLALA TREGO CO., KS	KLIENF. FM WOOD MT. S. SASKATCH	CUNNINGHAM COLTER TETON CO, WY
HEMPHILLIAN					*C. vasquezi* ● Jacobs, 1977						
CLARENDONIAN	LATE								*C. sholwelli* ● *C. pisinnus* ● Wilson, 1968		
	EARLY	*C. dentalis* ● *C. esmeraldensis* ● Hall, 1930 Clark et al., 1964		↑ ? *C. loxodon* ● Wood, 1936 Clark and others, 1964 ? ↓							
BARSTOVIAN	LATE		*C.* sp. Sutton, 1977			*C. niobrariensis* ● *C. kelloggae* ● Hoffmeister, 1959	*C. kelloggae* Klingener, 1968	*C. kelloggae* Korth, 1980		*C. kelloggae* Storer, 1975	*C. kelloggae*

Fig. 24.—Geographic and stratigraphic range of *Copemys* east of California and Oregon.

for which an unworn M^3 is known, the protocone is the only prominent cusp.

The sizes of all cheek teeth from Jackson Hole most closely resemble the sizes in *M. alexandrae.* Most M_1's and M_2's are slightly larger in the Jackson Hole species and the P^4's are 20% smaller, but the differences are not statistically significant.

Discussion.—Chevron height has been shown to increase with time in *Entoptychus,* a geomyoid genus whose general molar pattern resembles that of *Mojavemys* (Rensberger, 1971). *Mojavemys magnumarcus* is therefore probably more advanced than *M. alexandrae,* a conclusion buttressed by the more lophate character of cusps in *M. magnumarcus.* The Jackson Hole species is about as advanced in these features as *M. lophatus.*

Family Cricetidae Rochebrune, 1883
Genus **Copemys** Wood, 1936

Copemys kelloggae (Hoffmeister), 1959
Plate VII A, B

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Figs. 23, 24.

Referred specimens.—M_1, UWBM 62819. Maxilla with M^1–M^3, UWBM 62821.

Measurements.—M_1: AP = 1.5 mm, T = 1.1 mm. M^1: AP = 1.6 mm, T = 1.0 mm. M^2, AP = 1.2 mm, T = 0.9 mm. M^3: AP = 0.8 mm, T = 0.8 mm. See also Hoffmeister (1959), Klingener (1968), Korth (1980), Storer (1975), and Barnosky (1983).

Description and comparison.—Lindsay (1972:fig. 40) illustrated the dental terminology used here. The size of M_1's from Jackson Hole resembles that in *C. dentalis* (1.5 mm AP, 1.1 mm T, n = 3), *C. russelli* from Barstow (mean = 1.48 mm AP, 1.04 mm T; OR = 1.37–1.51 mm AP, 1.00–1.12 T; n = 6), *C. pagei* from Barstow (1.49 mm AP, 1.08 mm T, n = 2), and *C. kelloggae* from Cherry Co. (1.5 mm AP, 1.16 mm T, n = 1), Norden Bridge (mean = 1.47 mm AP, 1.05 mm T; OR = 1.4–1.6 mm AP, 1.0–1.2 mm T; n = 9), and Kleinfelder Farm (mean = 1.55 mm AP, 1.1 mm T; OR = 1.36–2.06 mm AP, 0.84–1.28 mm T; n = 46). The size of the M^1 from Jackson Hole falls within the size ranges of M^1's in these same species, although it is smaller than the mean in most cases: *C. dentalis* from Black Butte (mean = 1.54 mm AP, 1.00 mm T; OR = 1.46–1.68 mm AP, 0.94–1.05 mm T; n = 9), *C. russelli* from Barstow (mean = 1.73 mm AP, 1.13 mm T; OR = 1.60–1.85 mm AP, 1.10–1.20 mm T; n = 10 AP, 12 T), *C. pagei* from Barstow (mean = 1.52 mm AP, 0.99 mm T; OR = 1.48–1.55 mm AP, 0.92–1.05 mm T; n = 2), *C. pagei* from Quartz Basin (mean = 1.63 mm AP, 1.03 mm T; OR = 1.51–1.74 mm AP, 0.93–1.15 mm T; n = 23), and *C. kelloggae* from Norden Bridge (mean = 1.75 mm AP, 1.15 mm T; OR = 1.7–1.8 mm AP, 1.1–1.2 mm T; n = 2), Annies Geese Cross Quarry (1.71 mm AP, 1.12 mm T; n = 1), and Kleinfelder Farm (mean = 1.81 mm AP, 1.21 mm T; OR = 1.58–

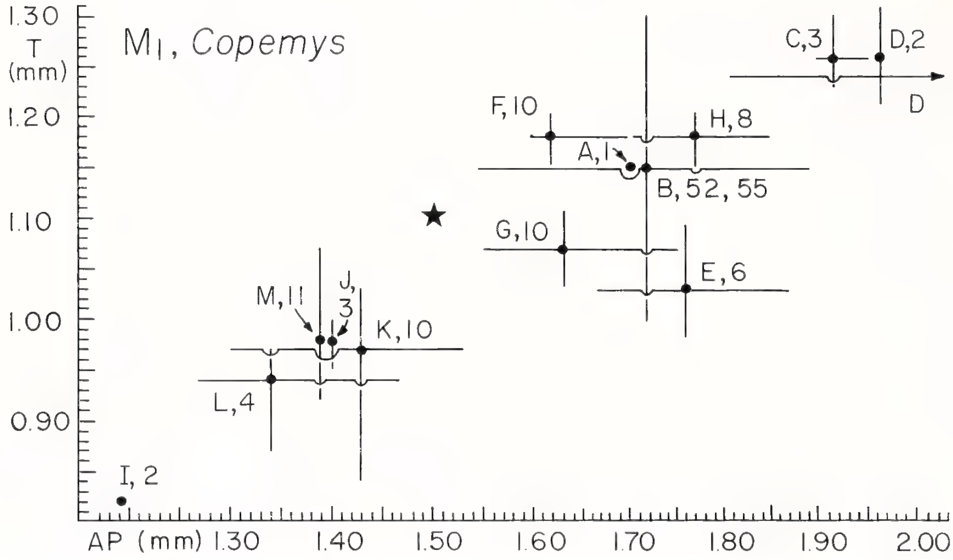


Fig. 25.—Bivariate plot of length (AP) vs. width (T) of M_1 for species of *Copemys* in which teeth are larger or smaller than teeth from Jackson Hole. Dot shows mean, lines show observed range (OR) of measurements from each locality. Numbers after letters indicate sample size; when two numbers are present the first is for AP, the second for T. Data compiled from sources listed in Figures 23 and 24. Abbreviations: *—Jackson Hole specimen. A—*Copemys loxodon* from New Mexico. B—*C. longidens,* Barstow. C—*C. esmeraldensis,* Barstow. D—*C. esmeraldensis,* Esmeralda. E—*C. esmeraldensis,* Black Butte. F—*C. russelli,* Cuyama Badlands. G—*C. tenuis,* Barstow. H—*C. barstowensis,* Barstow. I—*C. shotwelli,* Wakeeney. J—*C. pisinnus,* Wakeeney. K—*C. dentalis,* Black Butte. L—*C. vasquezi,* Redington. M—*C. pagei,* Quartz Basin. N—*C. niobrariensis,* Cherry Co. Observed range of AP for J = 1.35–1.44 mm, for M = 1.26–1.53 mm; of T for D = 2.13 mm.

2.20 mm AP, 0.97–1.39 mm T; n = 34). The Jackson Hole teeth are smaller than teeth of *C. loxodon, C. longidens, C. emeraldensis, C. russelli* from Matthews Ranch, *C. tenuis, C. barstowensis,* and *C. niobrariensis.* They are larger than in *C. shotwelli, C. pisinnus, C. vasquezi,* and the M_1's of *C. dentalis* from Black Butte and *C. pagei* from Quartz Basin (Figs. 25, 26).

The M_1 from Jackson Hole (UWBM 62819) (Pl. VII B) resembles specimens of *C. kelloggae* from Kleinfelder Farm, Saskatchewan, particularly ROM 6539 (Storer, 1975:fig. 58C). UWBM 62819 differs from the type of *C. kelloggae* only in the slightly less prominent and more worn hypoconulid, and more pronounced anterior cingulid. The Jackson Hole specimen is similar to referred specimens of *C. kelloggae* (UMMP 53029) (Klingener, 1968) from near the type locality in development of the anterior cingulid and hypoconulid. *C. dentalis, C. russelli,* and *C. pagei* lack a hypoconulid. UWBM 62819 and other *C. kelloggae* have a prominent mesolophid and ectolophid, unlike *C. dentalis* and most specimens of *C. pagei* (Shotwell, 1967*a*). UWBM 62819, like M_1 of *C. kelloggae,* differs from *C. russelli* in the lingually connected anteroconid and metaconid, and absence of a mesostylid. Unlike *C. tenuis,* but resembling the condition in *C. kelloggae,* UWBM 62819 is relatively wide and has a wide anteroconid.

The anterocone of the M^1 from Jackson Hole (UWBM 62821) is bilobed (Pl. VII A). Division remains even after a moderate amount of wear. The paralophule is small but evident. The incipient, very short mesoloph is pressed against the posterior flank of the paracone. The tooth lacks a mesostyle. The metacone joins the hypocone along the tooth's posterior margin. The posterior cingulum is not prominent and merges with the metacone and hypocone after slight wear. Morphology falls within the range of variation for *C. kelloggae* from Saskatchewan (Storer, 1975) and resembles the single M^1 of *C. kelloggae* that is known from Knox County, Nebraska (Korth, 1980). UWBM 62821 differs from the Knox County tooth only in having a more prominently bilobed anterocone and a paralophule. Both of these characters commonly vary in species known by large samples. The M^1 from Jackson Hole, like the Knox County tooth, lacks a long mesoloph, whereas M^1 of *C. dentalis, C. russelli, C. pagei,* and *C. tenuis* commonly has a well developed mesoloph.

On M^2 of UWBM 62821 (Pl. VII A), the anterior cingulum is weaker lingually than on a referred M^2

of *C. kelloggae* from Knox County, Nebraska (Korth, 1980). UWBM 62821, like the Nebraska M^2, differs from Saskatchewan specimens of *C. kelloggae* (Storer, 1975) in lacking a prominent mesoloph, and in having a narrower posterior border.

The anterior portion of M^3 of UWBM 62821 essentially resembles that of M^2, but the anterior cingulum is slightly closer to the paracone (Pl. VII A). A shallow valley exists between the protocone and hypocone, similar to that in *C. pagei* (Shotwell, 1967*a*). The protocone, reduced hypocone, and metacone posteriorly border a central lake that is intermediate in size between that in illustrations of *C. pagei* and the smaller lake in *C. dentalis* (Shotwell, 1967*a*).

Family Eomyidae Deperet and Douxami, 1902
Genus ***Pseudotheridomys*** Schlosser, 1926

Pseudotheridomys cf. ***P. pagei*** Shotwell, 1967
Plate VII C

Locality.—Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Range of North American species.—Hemingfordian: Martin Canyon Quarry A of Logan County, Colorado (*P. hesperus* Wilson, 1960). Vedder fauna of Santa Barbara County, California (*P. cuyamensis* Lindsay, 1974). Batesland fauna of Bennett County, South Dakota (*P.* sp., Martin, 1976). Late Barstovian: Quartz Basin and Red Basin faunas of Malheur County, Oregon (*P. pagei* Shotwell, 1967*a*).

Referred specimen.—P^4 or M^1, KUVP 17486.

Measurements.—AP = 1.0 mm. T = 1.0 mm.

Description and comparison.—KUVP 17486 (Pl. VII C) differs from P^4 and M^1 in *P. pagei* mainly in its labial closure of the anterior valley. The valley remains open until late stages of wear in *P. pagei* (Shotwell, 1967*a*:9). The mesoloph of KUVP 17486 is long but does not quite reach the labial edge of the tooth, as in the P^4 of *P. pagei. P. hesperus* has a very short mesoloph. The Jackson Hole specimen more closely resembles the M^1 than the P^4 of *P. pagei* in being nearly square. In KUVP 17486 and teeth of *P. pagei,* the metaloph and mesoloph are connected, in contrast to the unconnected condition in *P.* sp. from the Batesland Formation and *P. hesperus. P. hesperus* usually lacks such connection in unworn teeeth but the two lophs join with wear.

Discussion.—KUVP 17486 resembles teeth in *P. pagei,* except for closure of the anterior valley at an earlier stage of wear. Closure of the valley varies in *P. hesperus,* which is known by larger samples (Martin, 1976:83). The Jackson Hole species and *P. pagei* appear closely related if not conspecific. Referral of the Jackson Hole specimen is tentative because of the small sample size.

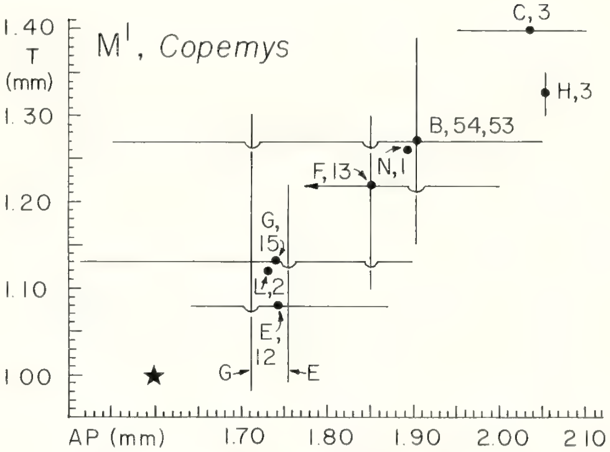


Fig. 26.—Bivariate plot of length (AP) versus width (T) of M^1 for species of *Copemys* in which teeth are larger or smaller than teeth from Jackson Hole. Observed range of AP for F = 1.10–2.00 mm. See Fig. 25 for additional explanation.

Family Zapodidae Coues, 1875
Subfamily Sicistinae Allen, 1901
Genus ***Schaubeumys*** Wood, 1935

Schaubeumys, species indeterminate

Localities.—North Pilgrim 2, UWBM loc. C0237. Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Range of genus.—Arikareean through Barstovian of Great Plains, exclusive of this occurrence. See Korth (1980) for a recent and comprehensive synopsis.

Referred specimens.—M_2, UWBM 62726 from loc. C0237. M^1 or M^2, KUVP 17485, UWBM 62822, 62824 from loc. C0236.

Discussion.—The referred molars from Jackson Hole show cusp morphology typical of *Schaubeumys* and *Plesiosminthus* (see Green, 1977; Black, 1958; Wilson, 1960; Engesser, 1979; Korth, 1980). Referral of the Jackson Hole material to *Schaubeumys* rather than *Plesiosminthus* is based on large size of the teeth (AP = 1.3–1.4 mm for M^1 (?)–M^2, 1.5 mm for M_2; T = 1.2–1.4 mm for M^1 (?)–M^2, 1.2 mm for M_2). Teeth of the only species of *Plesiosminthus* in North America, *P. clivosus* (Korth, 1979), are considerably smaller (AP = 1.1–1.3 mm for M^1, 1.0–1.1 mm for M^2, 1.1–1.2 mm for M_2; T = 0.9–1.2 mm for M^1, 0.9–1.0 mm for M^2, 0.8–1.0 mm for M_2) (Green, 1977). The nature of the Jackson Hole material combined with extreme variability within species of *Schaubeumys* (Green, 1977) precludes species assignment.

Table 14.—*Dental measurements,* Parahippus tyleri, *CMNH 21617, Colter Formation.*

Tooth	AP	T	C	Wear stage
Upper Teeth				
P or M	—	24	19	moderate
P or M	19	24	17	pronounced
Lower Teeth				
Left ramus				
P_3	18	12	10	pronounced
P_4	17	12	10	pronounced
M_1	17	10	7	pronounced
M_2	17	9	10	moderate
M_3	21	7	14	very slight
Right ramus				
P_3	18	12	10	pronounced
P_4	17	12	10	pronounced
M_1	16	11	—	broken
M_2	17	9	9	moderate
M_3	22	7	14	very slight

Explanation of measurements for upper teeth:
AP Taken at base of tooth, greatest distance from anterior part of parastyle to posterior part of metastyle
T Taken at base of tooth, greatest distance from lateral part of mesostyle to center of lingual margin
C Taken parallel to lateral ribs, height of crown from enamel-dentine border to metacone at occlusal surface.

Explanation of measurements for lower teeth:
AP Taken at base of crown, greatest distance from anterior part of paraconid to posterior part of entoconid
T Taken at base of crown, perpendicular to lingual margin, widest distance across talonid
C Taken perpendicular to occlusal surface, height of crown from enamel-dentine border to metaconid-metastylid complex at occlusal surface.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Merychippus* Leidy, 1857

***Merychippus*, species indeterminate**
Plate VII E, G

Locality.—Cunningham Hill, UWBM loc. C0236.
Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian of North America.

Referred specimens.—KUVP 40359a, fragment of upper cheektooth. KUVP 40359b, mandible with P_4, M_1, M_3. KUVP 40359c, isolated lower cheektooth. UWBM 62814, unworn P^2 (?).

Measurements (in mm).—KUVP 40359a, AP = 19. KUVP 40359b: P_4, AP = 20, T = 16; M_1, AP = 18, T = 16; M_3, AP = 25, T = 12; tooth row from anterior M_1 to posterior M_3 = 81. KUVP 40359c, AP = 21, T = 17. UWBM 62814, AP = 22, T = 9.

Description and comparison.—All but KUVP 40359c (Pl. VII E, G) are at stages of wear that make meaningful comparisons impossible. KUVP 40359c cannot be differentiated from comparably worn *M. republicanus* (Niobrara River Fauna), or *M. californicus* (Coalinga). The occlusal pattern of KUVP 40359c bears closest resemblance to that in *M. republicanus.* KUVP 40359c differs from *M. proplacidus* in possessing more prominent roots, from *M. intermontanus* in smaller size and lower crowns, from *M. insignus, M. calmarius, M. seversus* in lacking insertion of the labial V between the metaconid-metastylid complex, from *M. eohipparion* in larger size, from *M. carrizoensis* and *M. primus* in possessing a narrower labial V that does not insert between the metaconid-metastylid complex, from *M. gunteri* in higher crowns and larger size, and from *M. brevidontus* in higher crowns.

Discussion.—These horse teeth fall well within the range of variation exhibited by Barstovian and Clarendonian species of *Merychippus.*

Genus ***Parahippus*** Leidy, 1858

Parahippus tyleri Loomis, 1908
Plate VII D, F, H, I

Merychippus sp. Sutton and Black (1972), in part.
Merychippus sp. Love, McKenna and Dawson (1976), in part.
Parahippus tyleri Sutton and Black (1972), in part.
Parahippus tyleri Love, McKenna and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.
Age.—Early Hemingfordian.

Range of species.—Early Hemingfordian Runningwater Formation, Nebraska (questionable type locality, Sutton and Black, 1972).

Referred specimens.—CMNH 21617a, 2 upper cheek teeth. CMNH 21617b, left and right mandible with P_3–M_3.

Measurements.—Table 14.

Description and comparison.—Upper teeth from Jackson Hole, like fossils of *P. tyleri* from the Runningwater Formation (F:AM 173-1480, 385-2414, 200-2473, 109856) are distinct from teeth of most other species of *Parahippus* in large size, high crowns, and the presence of cement (Pl. VII H, I). CMNH 21617a and Runningwater specimens of *P. tyleri* differ from teeth of *P. avus* in having a less bulbous protocone, smaller hypostyle, and one or two less plications on the metaloph. CMNH 21617a resembles a specimen from Chalk Cliffs (McKenna, 1955) in simple plications, but is higher crowned with a less bulbous protocone.

The lower teeth (Pl. VII D, F) have the typically rounded labial margins of *Parahippus tyleri* like referred specimens from the Runningwater Formation (F:AM 109856, 393-2787). A prominent external cingulum is present. On M_3 cement partially fills the interstices between the protoconid and hypoconid, the hypoconid and hypoconulid, and the metastylid and entoconid. As in the upper dentition, the crowns are relatively high in specimens from Jackson Hole and *P. tyleri* from the Runningwater Formation. The two nearly unworn M_3's measure 14 mm from the enamel-dentine border at the base of the crown to the top of the metaconid. The high crowns, large size, and presence of cement of M_3 suggest that the upper and lower teeth from Jackson Hole are from the same species.

Discussion.—The type locality for *P. tyleri* is not known, but is probably within the Runningwater Formation (Sutton and Black, 1972, from communication by M. F. Skinner). Several referred specimens of *P. tyleri* (F:AM 173-1480, 385-2414, 200-2473, 109856, 393-2787) have been found in the Runningwater Formation.

Order Artiodactyla Owen, 1848
Family Merycoidodontidae Thorpe, 1923
Subfamily Merychyinae Simpson, 1945
Genus ***Merychyus*** Leidy, 1858

Merychyus arenarum Cope, 1884
Plate VIII A

Locality.—East Pilgrim 11, UWBM loc. C0239.

Age.—Late Arikareean.

Range of species.—Late Arikareean of Nebraska and Wyoming (Marsland Formation), and Lemhi Valley of Idaho (Table 15).

Referred specimen.—UWBM 63621, fragments of skull with M^2–M^3, humerus, 2 distal radii and ulnae, vertebra, probably from single individual.

Description and comparison.—UWBM 63621 is larger than specimens of *M. minimus, M. calaminthus, M. jahnsi,* and *M. crabilli,* evidenced by orbital diameter (measurement A, Pl. VIII) and length of M^3 (Table 15). In UWBM 63621, the orbit is nearly square and the zygomatic arch is laterally compressed, unlike the rounder orbits and flared zygomatic arches of *M. elegans, M. siouxensis,* and *M.* (*Metoreodon*). UWBM 63621 further differs from *M.* (*Metoreodon*) in the deeper zygomatic arch (Pl. VIII A, Table 15, ratio B/A). In *M. siouxensis* and *M. verrucomalus,* the arch is even deeper; the arch in *M. verrucomalus* also differs in having a distinct tuberosity (Stevens, 1970). The Jackson Hole specimen cannot be distinguished from *M. arenarum.* The orbital region of UWBM 63621 closely resembles that in skulls of *M. arenarum* from the Lemhi Valley, Idaho (AMNH 44827, 44829, 44830), from the type area at Platte County, Wyoming (AMNH 8145, 8149, F:AM 33374, 34403, 44583), and from Goshen County, Wyoming (F:AM 44598, 43288, 43270, 44533A).

***Merychyus,* species indeterminate**

M. arenarum Colbert (1943).
M. sp. Schultz and Falkenbach (1947).
M. sp. Love (1956).
M. arenarum Black (1968).
M. sp. Sutton and Black (1972).
M. elegans Love, McKenna, and Dawson (1976).

Localities.—Northwest bank of East Pilgrim Creek between outcrops 11b and 5 (Saunders locality).

Age.—Hemingfordian?

Range of genus.—Arikareean to early Barstovian of Nebraska, Wyoming, Idaho, South Dakota, California, Colorado, Table 15.

Referred specimens.—AUG-V120, rostrum and mandible with complete dentition. (This specimen has recently been located at the AMNH, where it is now housed as AMNH 89677.)

Description and comparison.—AUG-V120 was not available for inspection. Descriptions and illustrations by Colbert (1943) and Schultz and Falkenbach (1947) suggest that the specimen is larger than skulls of *M. minimus. M. verrucomalus,* and all Arikareean species of *Merychyus* except *M. siouxensis.* AUG-V120 differs from *M. siouxensis* in its smaller upper canines, shorter dental series from P^1 to M^3, and more convex rostrum between the incisors and nasals. Unlike M^1 in *M. arenarum,* that in AUG-V120 is relatively short (Colbert, 1943). Schultz and Falkenbach felt that AUG-V120 differed from species of *M.* (*Metoreodon*) in lacking "suggested cusps" on P_2–P_4. More detailed descriptions of these differences were not given. AUG-V120 most closely resembles skulls of *M. elegans* in dimensions and dental morphology, but is slightly narrower (Schultz and Falkenbach, 1947).

Discussion.—The exact geographic position of AUG-V120 is unknown, but must lie stratigraphically between Units 5 and 28. The original locality description places the fossil, which was found *in situ,* "in an eroding slope on the northwest bank of the south [=east] fork of Pilgrim Creek, one mile above the juncture of this fork with the north fork" (Colbert, 1943:298). Outcrops 5, 8, 8B, and 11B fit this description best (Fig. 2). Outcrop 5 is the most productive Miocene site along East Pilgrim Creek. Scraps of bone occur at outcrop 8. Beds in outcrop 11B correlate with Unit 5, which yielded a skull of *Merychyus arenarum* (UWBM 63621) from nearby outcrop 11.

Table 15.—*Comparison of characters in specimens of* Merychyus. *See explanation.*

		Characteristic						
Age and region	Specimen	Size of orbit (A)	Depth of zygoma (B)	B/A	Shape of orbit	Ventral zygoma	Humerus LEN/WID	M^3 AP/T
		Jackson Hole Species						
Wyoming	UWBM 63621	29	23	0.79	S	ZCS	92 mn/20	22/16
	AUG V-120	—	15	—	—	—	—	19/—
Late Hemingfordian and Early Barstovian (See Note 1 in explanation) Nebraska		*Merychyus (Metoreodon) relictus*						
	F:AM 33635	—	21	—	—	—	—/22	—
	F:AM 43078	22	14	0.64	CRA	ZF	—	20/16
	F:AM 34319*	26	14	0.53	CRA	ZF	—	21/16
Early Hemingfordian (See Note 2 in explanation) Nebraska		*Merychyus elegans*						
	UNSM 7-10-9-38	26	17	0.65	E-R	ZFR	—	22/16
	UNSM 3-5-8-36	26	22	0.84	E-R	ZFR	—	20/16
		Merychyus verrucomalus						
	See Stevens, 1970	24	21–31	0.91	R	T	—/26	$\frac{18.5\text{–}22.1}{14.6\text{–}16.1}$
Late Arikareean (see Note 3 in explanation)		*Merychyus arenarum*						
	AMNH 8146*	30	19	0.63	RP	ZF	—	19/16
	Range	21–31	11–25	0.44–0.95	—	—	—	16–24/12–18
Nebraska, Wyoming, Idaho	Mean	26.2	18.3	0.67	—	—	—	20.09/15.34
	Std. dev.	2.42	2.89	0.44	—	—	—	1.78/1.83
	No. specimens	45	46	44	—	—	—	41/38
	F:AM 43277	—	—	—	—	—	130/24	—
	F:AM 43279	—	—	—	—	—	120/28	—
	F:AM 44827	—	—	—	—	—	110/26	—
		Merychyus minimus						
Nebraska, Wyoming, South Dakota	CMNH 1466*	22	16	0.72	R	ZCS	—	20/14
	F:AM 33364	20	18	0.90	S	ZCS	—/20	18/14
	F:AM 44610	—	—	—	—	—	—/16	—
Arikareean (See Note 4 in explanation)		*Merychyus calaminthus*						
	LACM 1383	—	—	—	—	—	—	15.5/11.8
		Merychyus jahnsi						
California	LACM 1382	—	—	—	—	—	—	13.6/12.0
		Merychyus crabilli						
	UNSM 1-1-7-33*	—	15	—	—	—	—	—
	F:AM 45384A	24	14	0.58	S	ZF	—	18/14
	F:AM 4538Z4	—	—	—	—	—	100/23	—
	F:AM 45384Z5	—	—	—	—	—	90/22	—
	Range in 10 specimens from type locality (Schultz and Falkenbach, 1947:Chart 3)							$\frac{15.2\text{–}18.0}{11.7\text{–}13.7}$
		Merychyus siouxensis						
Nebraska	AMNH 13774	22	19	0.86	R	ZF	—	22/18

See Plate VIII for explanation of measurements. Except for the Jackson Hole specimens, *M. arenarum* skulls and teeth, and *M. verrucomalus,* measurements are from tables and illustrations in Schultz and Falkenbach (1947).

Abbreviations:

S = square.
mn = minimum.
E-R = elongate anteroposteriorly and round.
R-P = round posteriorly.
ZCS = zygomatic arch laterally compressed and slender in ventral view.
ZFR = zygomatic arch laterally flared and robust in ventral view.
ZF = zygomatic arch laterally flared in ventral view.
CRA = orbit compressed anteroposteriorly and round.

Table 16.—*Stratigraphic occurrence of species of* Merycochoerus.

Age	Species and formation	Location
Early Hemingfordian	*Merycochoerus proprius proprius*	
	Runningwater Formation[1]	Nebraska
	Merycochoerus proprius magnus	
	Runningwater Formation?[2]	Nebraska
	Arikaree Formation[3]	Colorado (Martin Canyon)
Late Arikareean	*Merycochoerus matthewi*	
	Marsland Formation[4]	Nebraska and Wyoming
	Rosebud Formation[5,6]	South Dakota

[1] Schultz and Falkenbach, 1940 (=Upper part of Marsland Formation).
[2] Schultz and Falkenbach, 1940 (Stratigraphic position uncertain, but not found with *M. matthewi,* which is confined to the "lower part of the Marsland Formation [p. 289]; intermediate in evolutionary stage between *M. matthewi* and *M. proprius proprius*).
[3] Galbreath, 1953 (="Pawnee Creek Formation").
[4] Schultz and Falkenbach, 1940 (=Lower part of Marsland Formation).
[5] MacDonald, 1963.
[6] MacDonald, 1970.

Subfamily Merycochoerinae Schultz and Falkenbach, 1940

Genus *Merycochoerus* Leidy, 1858

Merycochoerus proprius magnus (Loomis, 1924)

Plate VIII B

Merycochoerus? Love (1956), in part.
Merycochoerus? Black (1968), in part.
Merycochoerus? Sutton and Black (1972), in part.
Ticholeptus Love (1956).
Brachycrus Love, McKenna, and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.
Age.—Early Hemingfordian.

Range of genus.—Table 16.

Referred specimen.—USNM 17919, in part. Rostrum and anterior mandible, vertebrae, fragments of humerus, radius, ulna, pelvis, femur, tibia, fibula, metapodials, podials.

Description and comparison.—Unlike the condition in *Ticholeptus, Merychyus,* and *Ustatochoerus,* the infraorbital foramen is located above M^1 in USNM 17919 (Pl. VIII B). *Merychyus* further differs in being more hypsodont. In lateral view, *Ticholeptus* shows a more gentle slope and straighter dorsal profile of the maxilla and premaxilla between the incisors and naries. In contrast, the lateral profile of the rostrum in USNM 17919 curves convexly between incisors and nasal vacuity, forms a flat platform in the vicinity of the naries, then curves sharply dorsad (Pl. VIII B). In these respects, it resembles *Mediochoerus* and *Merycochoerus. Brachycrus* differs in possessing a facial cavity and infraorbital foramen above M^2. All of these characters are illustrated by Schultz and Falkenbach (1940, 1941, 1947).

In proportions of the rostrum (ratios NV/PM, DEPTH2/DEPTH1, DEPTH2/C-M), USNM 17919 more closely resembles *Merycochoerus* than *Mediochoerus* (Table 17). The relatively long premaxillary suture ending in a dorsal protrusion (PR, Pl. VIII B) is particularly characteristic of *Merycochoerus proprius proprius* and *M. proprius magnus.* The rostrum in the Jackson Hole specimen begins to increase in depth between P^4 and M^1. In this respect it resembles *Mediochoerus blicki* and a referred specimen of *Merycochoerus proprius magnus* (F:AM 37520). The depth increase begins slightly more posterior, that is, over M^1, in the type of *Merycochoerus proprius magnus,* over posterior M^1 or anterior M^2 in *M. proprius proprius,* and over P^3 in *M. matthewi.*

The occluded dentition in the Jackson Hole specimen prevents detailed description. The upper canine is about the same size as the incisor, differing from the relatively large canines of *M. proprius proprius, M. proprius magnus,* and *M. matthewi.* A 5 mm diastema separates P^1 from the canine and P^2. P^1, composed of a single oblique blade, is the largest antemolar and P^2 possesses a small posterior shelf. Other premolars and the incisor are broken. The molars are relatively brachyodont, with the distance from the enamel-dentine border to the tip of the

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Note 1.—*M.* (*Metoreodon*) *relictus* was found in the "Lower Snake Creek" of Schultz and Falkenbach (1947), which probably equates with the early Barstovian Olcott Formation of Skinner et al. (1977). *M.* (*M.*) *relictus taylori* occurs in the late Hemingfordian Sheep Creek Formation of Skinner et al. (1977).

Note 2.—Type of *M. elegans* found in "upper Marsland Fm." of Schultz and Falkenbach (1947) (=Runningwater Formation of McKenna, 1965). Referred specimens with locality data from Dunlap Camel Quarry NE of Hemingford, Sand Canyon Quarry (Sand Canyon locality), Potter Quarry (Sand Canyon drainage system), Hemingford Quarry 2, 7B, 11B, 12A, 12C, 12D, 17, 21, 23 (all Nebraska), and Martin Canyon, Colorado.

Note 3.—Cited as "Lower Marsland" by Schultz and Falkenbach (1947), here considered correlative to the "Upper Harrison beds" of Hunt (1985).

Note 4.—Cited as "Harrison equivalent" by Schultz and Falkenbach (1947).

Table 17.—*Measurements of* Merycochoerus *and* Mediochoerus.

Specimen and statistics	Measurement*													
	PM	NV	NV/PM	DEPTH1	DEPTH2	C-M	DEPTH2/DEPTH1	DEPTH2/C-M	MND	ROSLEN	M^1	M^2	HUM WID	TIB LEN
							MERYCOCHOERUS (Colter Formation)							
USNM 17919	53	26	0.49	55	44	49	0.80	0.89	34	64	18	26a	51	121
							MERYCOCHOERUS PROPRIUS PROPRIUS							
F:AM 42469[1]	108	38	0.35	118	70	73	0.59	0.96	54	124	22	32	60–66	124–136
Mean, N = 7	91.4	34.6	0.39	109.6	70.3	—	0.66	—	—	—	—	—	—	—
Std. dev.	21.1	6.2	0.10	24.0	10.3	—	0.10	—	—	—	—	—	—	—
							MERYCOCHOERUS PROPRIUS MAGNUS							
AMNH 14242[1]	69	48	0.70	86	58	76	0.67	0.76	60	104	20	26	64	172
F:AM 37520	76	32	0.42	79	50	—	0.63	—	—	—	—	—	—	—
							MERYCOCHOERUS MATTHEWI							
AMNH 12970[1]	30	42	1.40	70	38	64	0.54	0.59	40	72	19	26	—	—
Mean, N = 6	36.1	48	1.34	78.3	42.8	—	0.57	—	—	—	—	—	—	—
Std. dev.	4.7	4.9	0.17	19.8	4.4	—	0.13	—	—	—	—	—	—	—
							MEDIOCHOERUS BLICKI							
F:AM 43172	33	40	1.21	55	32	47	0.58	0.68	—	52	18	24	—	—
F:AM 43173	35	29	0.83	—	36	—	—	—	—	—	—	—	—	—
							MEDIOCHOERUS JOHNSONI							
UNSM 2-11-8-36[2]	—	—	—	—	—	—	—	—	—	—	13	18	—	—
F:AM 24439	17	28	1.65	66	27	0.41	—	—	—	—	—	—	—	—

[1] Measurements from Schultz and Falkenbach, 1940.
[2] Measurements from Schultz and Falkenbach, 1941.
* See Plate VIII for explanation of measurements on skulls
HUM WID greatest width across distal portion of humerus.
TIB LEN greatest length along lateral edge of tibia.
a = at least.

Table 18.—*Measurements of* Desmatochoerus leidyi.

Measurement*	AMNH 89724	Other specimens†
Basal length of skull	295 mx	280–285
Maximum width of skull	176	—
P^1–M^3	145 mx	131–139
P_1–M_3	153 mx	148
M_3 AP	43 mx	38–39

* See Schultz and Falkenbach (1968:472) for definition of measurements.
† Measurements from Schultz and Falkenbach (1954).
mx maximum.

nearly unworn metacone on M^2 measuring 23 mm. The mesostyles are moderately developed.

The lower canines are nearly twice the size of the incisors, relatively larger than in *M. matthewi* but resembling other species of *Merycochoerus.* P^1 is nearly as large as the canine. Other teeth are either broken or too tightly occluded for safe separation. Epiphyses are not fused on the postcranial bones, indicating that the individual was young.

Discussion.—The long premaxillary suture, combined with an increase in rostrum depth between P^4 and M^1, cause referral to *M. proprius magnus.* Individual variation and young ontogenetic age easily account for the small canines and small size of the Jackson Hole specimen, especially in view of the variation known to occur within species of *Merycochoerus* (Shultz and Falkenbach, 1940:278).

The postcranial material here referred to this small individual of *Merycochoerus* may have been attributed to *Brachycrus* by previous workers (Love, 1956; Black, 1968; Sutton and Black, 1972). I refer it to *Merycochoerus* based on its close association with the skull, although postcranial morphology of *Brachycrus* and small specimens of *Merycochoerus* has not been shown to be diagnostic. In examining all of the oreodonts collected by Love in 1945, I found no other bones that could logically be attributed to *Brachycrus.*

Merycoidodontidae, species indeterminate

Merycochoerus? Love (1956), in part.
Merycochoerus? Black (1968), in part.
Merycochoerus? Sutton and Black (1972), in part.
Merycochoerus Love, McKenna, and Dawson (1976), in part.

Locality.—East Pilgrim 5, UWBM loc. C0240.
Age.—Early Hemingfordian.

Referred specimens.—USNM 17919, in part. Sacrum, 2 femora, 2 tibiae, articulated tarsals and metatarsals, probably from same individual.

Measurements (in mm).—Lateral length of 2 femora, 245, ±245. Lateral length of 2 tibiae, 151, 147.

Discussion.—The bones represent a large oreodont that approaches *Megoreodon, Desmatochoerus, Promerycochoerus, Merycochoerus,* or *Ustatochoerus* in size. These bones were recovered in association with those of the small *Merycochoerus proprius magnus* that is described above (J. D. Love, personal communication, 1980), but obviously represent a significantly larger individual.

Subfamily Desmatochoerinae Schultz and Falkenbach, 1954

Genus **Desmatochoerus** Thorpe, 1921

Desmatochoerus leidyi (Bettany, 1876)

Plate IX

Promerycochoerus leidyi Love, McKenna, and Dawson (1976).

Locality.—Emerald Lake SR, UWBM loc. C0241.
Age.—Late Arikareean.

Range of species.—Arikareean: John Day Formation of northeast Oregon (Bridge Creek, the Cove, Butler Basin) (Schultz and Falkenbach, 1954).

Referred specimens.—AMNH 89724, skull and mandible with dentition. Questionably referred, UWBM 63262, anterior portion of rostrum that may belong to same individual as AMNH 89724.

Description and comparison.—AMNH 89724 is referred to *Desmatochoerus* rather than *Promerycochoerus* on the basis of relatively narrow skull (less than 190 mm) (Table 18), narrow braincase, thin sagittal crest, small laterally compressed bullae, very robust dentition, robust styles, and laterally compressed paraoccipital processes. All species of *Promerycochoerus,* in contrast, show wide skulls (190–322 mm), inflated braincase, robust sagittal crest, large bullae, moderately heavy dentition, small styles, and laterally compressed paraoccipital processes (Schultz and Falkenbach, 1949, 1954).

AMNH 89724 cannot be differentiated from *Desmatochoerus leidyi* except for slightly larger size (Table 18). All measurements that indicate larger size, however, are maximum estimates because the premaxilla and posterior portions of the third molars are missing or distorted. Other species of *Desmatochoerus* are definitely smaller, with basal length not exceeding 270 mm (Shultz and Falkenbach, 1954:160).

Family Camelidae Gray, 1821

Genus **Aepycamelus** MacDonald, 1956

Aepycamelus, species indeterminate

Locality.—Two Ocean Lake, UWBM loc. C0238.
Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian (Wood et al., 1941).

Referred specimen.—UWBM 63267, portions of partially articulated vertebrae, humerus, radioulna, metacarpal, tibia, astragalus, phalanges of single individual.

Measurements (in mm).—Astragalus: Width, 43. Lateral length, 67. Medial length, 61.

Medial phalanx: Length, 90, Proximal width, 33. Distal width, 24.

Tibia: Distal width, 69.

Radius: Length, 510. Proximal width, 64. Transverse diameter at center of shaft, 48. Distal width, 62.

Composite radioulna: Length, approximately 593.

Metacarpal (?): Length, minimum 400 (broken). Transverse diameter, ±50.

Humerus: Distal width, 63.

Longest cervical vertebra (broken): Minimum length, 160. Narrowest diameter of centrum, 33.

Discussion.—The large size, long cervical vertebrae, and elongate, slender limb bones suggest the genus is *Aepycamelus.*

Genus **Oxydactylus** Peterson, 1904

?***Oxydactylus,*** **species indeterminate**

Locality.—East Pilgrim Creek between outcrops 11b and 5 (Saunders locality).

Age.—Hemingfordian.

Range of genus.—Arikareean, Hemingfordian (MacDonald, 1963, 1970).

Referred specimens.—AUG-V121, podials and fragmentary metapodial. (These specimens are now at the AMNH, catalogued as AMNH 101148.)

Discussion.—I have not examined this material and rely on the identification by Colbert (1943), who illustrated the specimens.

Family Antilocapridae Gray, 1866

Genus **Merycodus** Leidy, 1854

Merycodus, **species indeterminate**

Locality.—Cunningham Hill, UWBM loc. C0236.

Age.—Late Barstovian.

Range of genus.—Hemingfordian to Clarendonian (Wood et al., 1941).

Referred Specimen.—KUVP 17482, mandible fragment with worn M_2–M_3.

Measurements (in mm).—M_2: AP = 9, T = 6. M_3: AP = 1.3, T = 6.

RESULTS

At least 32 species of Miocene mammals occur in the Colter Formation and represent faunas of three distinct ages—Arikareean, Hemingfordian, and Barstovian. Faunal groups from different parts of the Colter are designated here as the Emerald Lake Fauna (late–early Arikareean age), the East Pilgrim Assemblage (includes three sparsely represented local faunas that range from the late Arikareean to the early Hemingfordian), and the Cunningham Hill Fauna (late Barstovian age).

Faunal Ages

Emerald Lake Fauna (late–early Arikareean)

The Emerald Lake Fauna consists of the species recovered from Unit 1 at Emerald Lake SR (UWBM loc. C0241) (Table 19). Except for a single oreodont rostrum, all of the fossils from the very limited exposure were reported by Love et al. (1976), and McKenna kindly made them available to me for examination. *Allomys cristabrevis,* new species, which is slightly more primitive than *Allomys harkseni* from the Monroe Creek Formation and decidedly more primitive than all but the oldest species from the John Day Formation (*A. cavatus,* Rensberger, 1983), implies correlation with about the middle of the *Meniscomys* Concurrent-range zone. Rensberger (1981) concluded that the other aplodontid, *Niglarodon* sp., suggests correlation with the top of the *Meniscomys* Concurrent-range Zone. Unit 1SR, therefore, probably falls somewhere within the upper half of this zone. The occurrence of *Desmatochoerus leidyi* and *Archaeolagus emeraldensis,* new species, is compatible. The only other reported specimens of *D. leidyi* occur within the John Day Formation, but precise locality data are lacking. Based on stage of evolution, Shultz and Falkenbach (1954, 1968) considered species of *Desmatochoerus* to range through strata contemporaneous with the Gering, Monroe Creek, and Harrison Formations. They considered *D. leidyi* to have come from strata "approximately equal in age to the Harrison Formation of the central Great Plains" (1954:185). *Archaeolagus emeraldensis,* new species, is morphologically most similar to, but perhaps slightly more advanced than, *A. ennisianus,* which is found in the John Day Formation (Dawson, 1958:42). More precise locality data for *A. ennisianus* are not available. Like *A. ennisianus, A. emeraldensis* possesses a longer P_3

Table 19.—*Faunal list for Emerald Lake Fauna.*

- Rodentia
  - Aplodontidae
    - *Niglarodon* sp.
    - *Allomys cristabrevis,* new species
- Lagomorpha
  - Leporidae
    - *Archaeolagus emeraldensis,* new species
- Artiodactyla
  - Merycoidodontidae
    - *Desmatochoerus leidyi*

and is smaller than average for late Arikareean *A.* cf. *A. macrocephalus* and early Hemingfordian *A. macrocephalus.* I follow Fisher and Rensberger (1972), Rensberger (personal communication, 1983), and Woodburne and Robinson (1977) in considering the upper half of the *Meniscomys* Concurrent-range Zone, and by inference Unit 1SR at Emerald Lake, to approximately correlate with 23.6 to 24.6 my on the radiometric scale. Radiometric dates of about 26 to 29 my have been determined near the base of the *Meniscomys* Concurrent-range Zone in the John Day and Gering Formations (Fisher and Rensberger, 1972; Evernden et al., 1964; Obradovich et al., 1973; Rose and Rensberger, 1983). The middle of the overlying *Entoptychus-Gregorymys* Concurrent-range Zone was K-Ar dated at 21.9 my in the Harrison Formation (Fisher and Rensberger, 1972; Evernden et al., 1964).

East Pilgrim Assemblage
(late Arikareean to early Hemingfordian)

Fossils from East Pilgrim 11 (UWBM loc. C0239), the Saunders locality, and East Pilgrim 5 (UWBM loc. C0240), comprise the East Pilgrim Assemblage (Table 20). The localities span a considerable stratigraphic distance, Units 5 through 28, but each produced few specimens. They are here artificially grouped into the same assemblage merely for convenience. Each locality is discussed separately, because differences in age are probable.

Table 20.—*Faunal lists for East Pilgrim Assemblage.*

East Pilgrim 5 local fauna (from Unit 28):
- Perrisodactyla
  - Equidae
    - *Parahippus tyleri*
- Artiodactyla
  - Merycoidodontidae
    - *Merycochoerus proprius magnus*
    - cf. *Merycochoerus*

Saunders local fauna (from between Unit 5 and 28):
- Artiodactyla
  - Camelidae
    - ?*Oxydactylus*
  - Merycoidodontidae
    - *Merychyus* (cf. *M. elegans*)

East Pilgrim 11 local fauna (from Unit 5):
- Artiodactyla
  - Merycoidodontidae
    - *Merychyus arenarum*

East Pilgrim 11 local fauna (late Arikareean), from UWBM loc. C0239, Unit 5.—The only specimen from this site, UWBM 63621, is an oreodont skull that cannot be differentiated from skulls of *Merychyus arenarum. M. arenarum* is known only from the Marsland Formation *sensu* McKenna (1965) (here considered equivalent to the "Upper Harrison" beds of Hunt, 1985) in the superposed sequence of the Great Plains, and from the Lemhi Valley of Idaho (Schultz and Falkenbach, 1947). Unit 5, like the Marsland Formation, is therefore considered late Arikareean in age (Hunt, 1985). The late Arikareean seems to correlate with about 19 to 23 my in the Great Plains. Dates on various ashes within the Arikaree Group bracket the major intra-Arikareean faunal change between 25 and 22 my to provide the lower limit (Hunt, 1985:194). For example, a 21.9 my date from near the middle of the Harrison Formation (Evernden et al., 1964) was determined from the Agate Ash approximately 10 m below a late Arikareean fauna. The upper limit—that is, the Arikareean-Hemingfordian boundary—appears younger than 19.2 m.y. as indicated by a fission-track date on the Eagle Crag Ash, which lies below the late Arikareean Niobrara Canyon local fauna (Hunt, 1985:177). Radiometric-age determinations associated with Hemingfordian faunas are consistent with placing the end of the Arikareean near 19 my. A date of 21.6 my was obtained between the late Arikareean Black Butte and early Hemingfordian Logan Mine faunas of the Hector Formation in California (Woodburne et al., 1974). The early Hemingfordian Boron local fauna in California occurs stratigraphically above dates ranging from 18.3 to 20.3 m.y. (Whistler, 1984). The late Hemingfordian Philips Ranch, California, and Split Rock, Wyoming, faunas are associated with K-Ar dates of 17.6 and 17.4 my, respectively (Evernden et al., 1964; Munthe, 1979*a*). The Philips Ranch fauna is above the dated rocks, and the Split Rock fauna is from strata above and below the dated sample.

Saunders local fauna (early Hemingfordian?), from East Pilgrim Creek, somewhere between Units 5 and 28.—The only biostratigraphically useful fossil, recovered by Roy Saunders in the 1930's, represents a species of *Merychyus* that differs from Arikareean species in larger size, smaller upper canines, or both. The specimen most closely resembles skulls of *Merychyus elegans,* an early Hemingfordian species.

East Pilgrim 5 local fauna (early Hemingfordian), from UWBM loc. C0240, Unit 28.—Examination of the only material known from this locality was possible through the courtesy of C. C. Black, M. R. Dawson, and R. J. Emry. *Parahippus tyleri* is represented by two upper cheek teeth (CMNH 21617a) and two mandibles with cheek teeth (CMNH 21617b). The upper teeth were previously referred to *Merychippus,* but are morphologically quite similar to other specimens of *P. tyleri* (for example, F:AM 173-1480, 385-2414, 200-2473, 109856), particularly in high crowns (for *Parahippus*), incomplete union of crochet and protoloph, large size, and very thin layer of cement. Lower teeth resemble those of referred *P. tyleri* (F:AM 109856, 393-2787) in high crowns, rounded labial margins, and cement only on M_3. The comparative specimens mentioned above are from the early Hemingfordian Runningwater Formation; the type of *P. tyleri* probably also comes from the Runningwater (Sutton and Black, 1972).

The species of oreodont found in Unit 28, *Merycochoerus proprius magnus,* occurs in the early Hemingfordian Martin Canyon Quarry A Fauna and, from what little stratigraphic data is available for Nebraska specimens, probably also in the Runningwater Formation (Schultz and Falkenbach, 1940). The horse and the oreodont suggest that the age of Unit 28 equates closest with that of the Runningwater Formation, as was also concluded by Sutton and Black (1972). Unit 28 is therefore considered early Hemingfordian age, which according to correlations discussed above ranges from about 18 to 19 my ago. Contrasting with earlier reports, no objective evidence suggests the presence of *Brachycrus* in the Unit 28 assemblage.

Cunningham Hill Fauna (late Barstovian)

By far the most diverse in Jackson Hole, the Cunningham Hill Fauna includes assemblages from Cunningham Hill (UWBM loc. C0236), North Pilgrim 2 (UWBM loc. C0237), and Two Ocean Lake (UWBM loc. C0238). Nearly identical faunules characterize the first two localities, and the single fossil from Two Ocean Lake is from a stratigraphic position close to that of Cunningham Hill. Similarities to other faunas that share genera (Fig. 27) imply a late Barstovian age for the Cunningham Hill Fauna. It is no older than Barstovian, based on the occurrence of *Copemys, Cupidinimus,* and *Mojavemys,* all of which appear first in the early Barstovian. It is no older than late Barstovian, because *Domninoides, Spermophilus, Petauristodon, Diprionomys agrarius,* and *Lignimus* are unknown in older faunas. The Cunningham Hill Fauna is probably not younger than late Barstovian because it includes *Oreolagus, Monosaulax,* and *Peridiomys,* which are taxa unknown in Clarendonian or younger faunas. *Petauristodon* occurs only in the *Copemys longidens* and the overlying *Copemys russelli* Assemblage Zones of the Barstow Formation (Lindsay, 1972), and *Domninoides* is present only in the *Copemys russelli* Assemblage Zone. A tuff near the boundary between these zones in the Barstow Formation yielded K-Ar dates of 13.6 to 13.8 my (Lindsay, 1972; Savage, 1977). On the Great Plains, a fission-track date of 11.6 my, or perhaps 13.6 my depending on how the glass standards are calculated, was determined from the Hurlbut Ash between the Niobrara River Fauna and the Norden Bridge Fauna (Skinner and Johnson, 1984:252). The Cunningham Hill Fauna shares with both faunas *Diprionomys agrarius, Copemys kelloggae,* and several genera (Fig. 27). It therefore seems likely that the Cunningham Hill Fauna falls between 12 and 14 my on the radiometric scale.

CORRELATIONS

Similarities in small mammals suggest that Unit 1 of the Colter Formation correlates with parts of the John Day, Deep River, and Monroe Creek Formations, Cabbage Patch beds, and with deposits containing the Peterson Creek local fauna (Figs. 28, 29). Large mammals suggest that Unit 5 correlates with the Marsland Formation, and Unit 28 with the Runningwater Formation. Formations that share many faunal elements with Unit O (=±69) and Unit 43 include parts of the upper Barstow, the Caliente, and Deer Butte, the Madison Valley, the Valentine, and the Wood Mountain Formations and the Butte Creek Volcanic Sandstone. Most other correlates listed on the charts (Figs. 28, 29) show faunal elements diagnostic of a given age, but do not share elements with the Colter faunas. For the sake of

LOCALITY / TAXON	JACKSON HOLE			HEMINGFOR. LATE						BARSTOVIAN EARLY					BARSTOVIAN LATE																CLARENDONIAN EARLY				CLARENDONIAN LATE				
	CUNNINGHAM HILL	NORTH PILGRIM 2	TWO OCEAN LAKE	HIDDEN TRSR. SPG.	VEDDER	WARM SPRING	SPLIT ROCK	BOX BUTTE	SHEEP CREEK	C. NEB. AZ. BARSTOW	MASCALL	VIRGIN VALLEY	EUBANKS	OLCOTT	P. STIR. AZ. BARSTOW	C. LONG. AZ	C. RUSS. AZ.	OTHER BARSTOW	DOME SPRING	TONAPAH	QUARTZ BASIN	RED BASIN	ANCENEY	FLINT CREEK	VIM PEETZ	KEENESAW	NORDEN BRIDGE	ANNIES GEESE X	NIOBRARA R.	KLEINFELDER FM.	MATTHEWS RNCH.	AVAWATZ	FISH LAKE V.	BURGE	NETTLE SPG.	BLACK BUTTE	MINNECHADUZA	WAKEENEY	WOLF CREEK
Domninoides cf. D. storeri		●															○				○		○						○	◑			○	○				○	○
Scalopoides sp. indet.	●				○																○	○								○						○			
Scalopini sp. indet.	●																																						
Oreolagus colteri n. sp.	●	●					○					○											○																
Hypolagus sp. indet.	●	●		○	○		?			○	○	○			○	○	○		○	○	○		○		○				○	○	○	○	○	○	○	○	○	?	○
Spermophilus nr. S. primitivus		●																			?	○	○	◑						○									
Tamias cf. T. ateles	●	●					○								◑	◑	◑			◑	○	○					?		○	○	◑				◑			?	
Petauristodon		●														○	○		○			○								○	○				○				
Monosaulax cf. M. curtus	●					?						○	○	○	○	○						○	◑				○		◑	○									
Perognathus furlongi	●	●					○			●					●	●	●		●				○				○	●	○		●				●	○			
Cupidinimus sp.	●	●								○					○	○	○						○				○	○	○	○		○	◑		○				
Peridiomys sp. indet.	●	●					○			○	○		○								○	○	○			○				○									
Diprionomys agrarius	●	●																									●	●	●	◑			○	●		○			
Proheteromys sp. indet.	●				○		○												○							○													
Lignimus transversus n. sp.	●	●																									◑	○		◑				○				○	
Mojavemys magnumarcus n. sp.	●	●								◑	○				◑	◑	◑				○																		
Copemys kelloggae	●									○					○	○	○		○	○	○	○	○				●	●	●	●	○	○	○		○	○		○	
Pseudotheridomys cf. P. pagei	●				○																◑	◑																	
Schaubeumys sp. indet.	●	●					○																	○			○	○		○									
Merychippus sp. indet.	●				○	○	○	○	○		○	○	◑	○				○	◑		○	○	○		○	○			◑	○				○			○		
Aepycamelus sp. indet.			●					○	○					○						○					○	?			○		○		○	○					
Merycodus	●						○	○	○			○								○	○	○	○							○	○	○	○		○			○	○

● Same species as at Jackson Hole

◑ Species similar in evolutionary stage

○ Same genus, species different or indeterminate

? Questionable occurrence of same genus

Fig. 27.—Faunal checklist and comparison of the Cunningham Hill Fauna, which includes fossils from North Pilgrim 2 (UWBM loc. C0237), Cunningham Hill (UWBM loc. C0236), and Two Ocean Lake (UWBM loc. C0238).

completeness, the Browns Park, North Park, and Troublesome Formations are included but placed mainly on the basis of radiometric dates. Only published data have been used to construct the charts. Placement of the Barstovian–Clarendonian boundary follows Webb (1969), while correlation of the radiometric chronology with most epochs, provincial ages, and concurrent-range zones agrees with Armentrout (1981) and Woodburne and Robinson (1977). Other sources, as well as dates culled mostly from Evernden et al. (1964), are listed on the charts. Where appropriate, these authors' correlations have been modifieid according to the IUGS constants for K-Ar dates set forth by Dalrymple (1979), and to take into account recent dates and stratigraphic work on the Great Plains (Hunt, 1985).

FAUNAL RELATIONSHIPS

At the generic level the Cunningham Hill Fauna resembles late Barstovian faunas from all three geo-

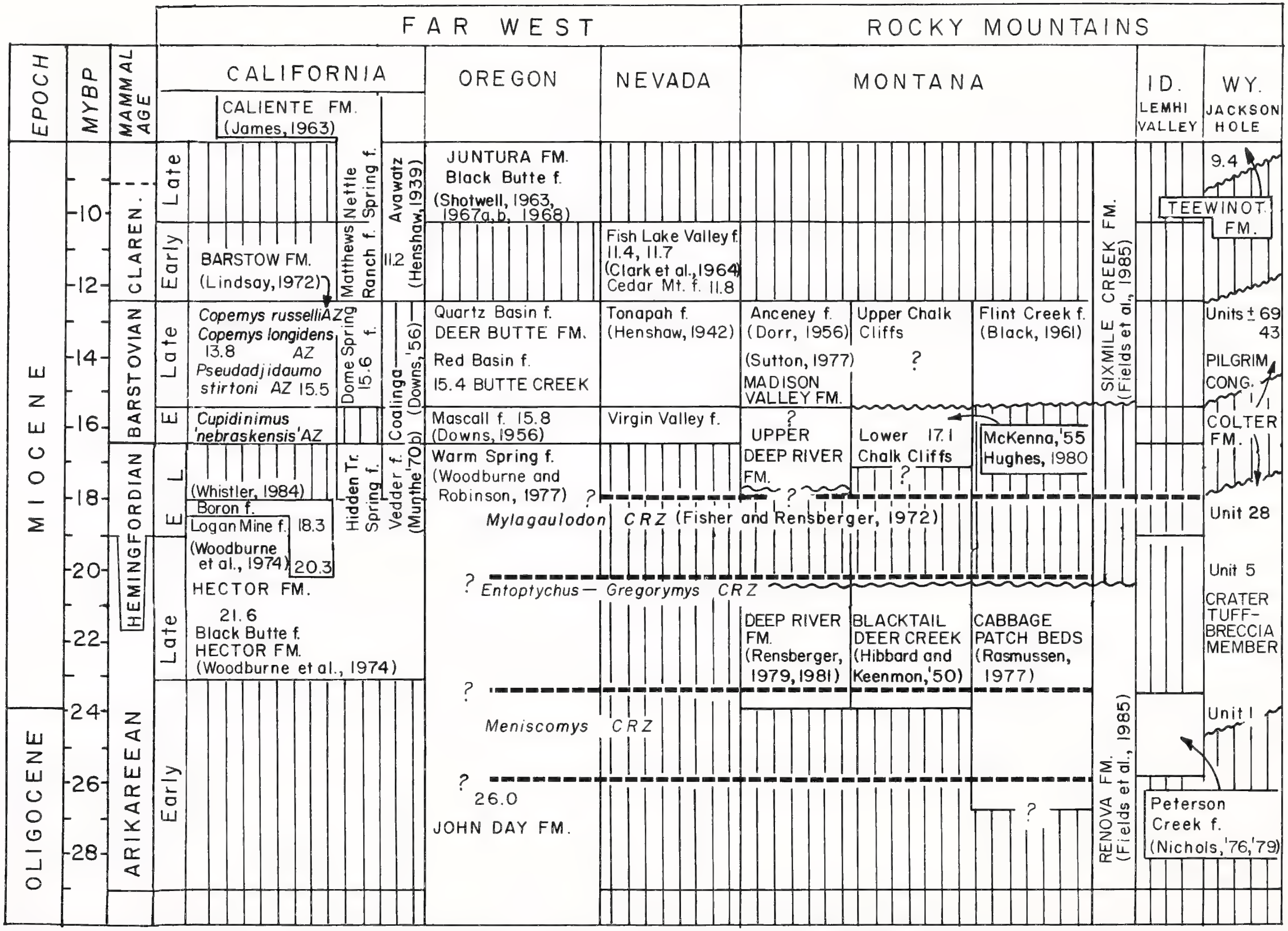

Fig. 28.—Biostratigraphic correlation of the Colter Formation and faunas with rocks (capital letters) and faunas (lower case) of the Far West and Rocky Mountains. Except for the Clarendonian-Hemphillian and the Arikareean-Hemingfordian boundaries, correlation of the radiometric chronology with epochs and mammal ages is from Armentrout (1981). In Jackson Hole, a K-Ar date of 9.4 my from 32 m below a Hemphillian mammal assemblage (Hibbard, 1970) suggests that the early Hemphillian may be about 1 my older than Armentrout places it. The Arikareean-Hemingfordian boundary is considered to be at least 2 my younger than Armentrout's assignment on the basis of Hunt's (1985) report of a 19.2 my date from below the typical late Arikareean Niobrara Canyon local fauna in Nebraska. Placement of concurrent-range zones is modified from Fisher and Rensberger (1972) and Woodburne and Robinson (1977) to conform with movement of the Arikareean-Hemingfordian boundary, and with Dalrymple's (1979) standards for calculation of K-Ar dates. Localities are sorted into the early or late part of provincial land-mammal ages, but closer correlation with the radiometric scale is not intended except where dates are listed.

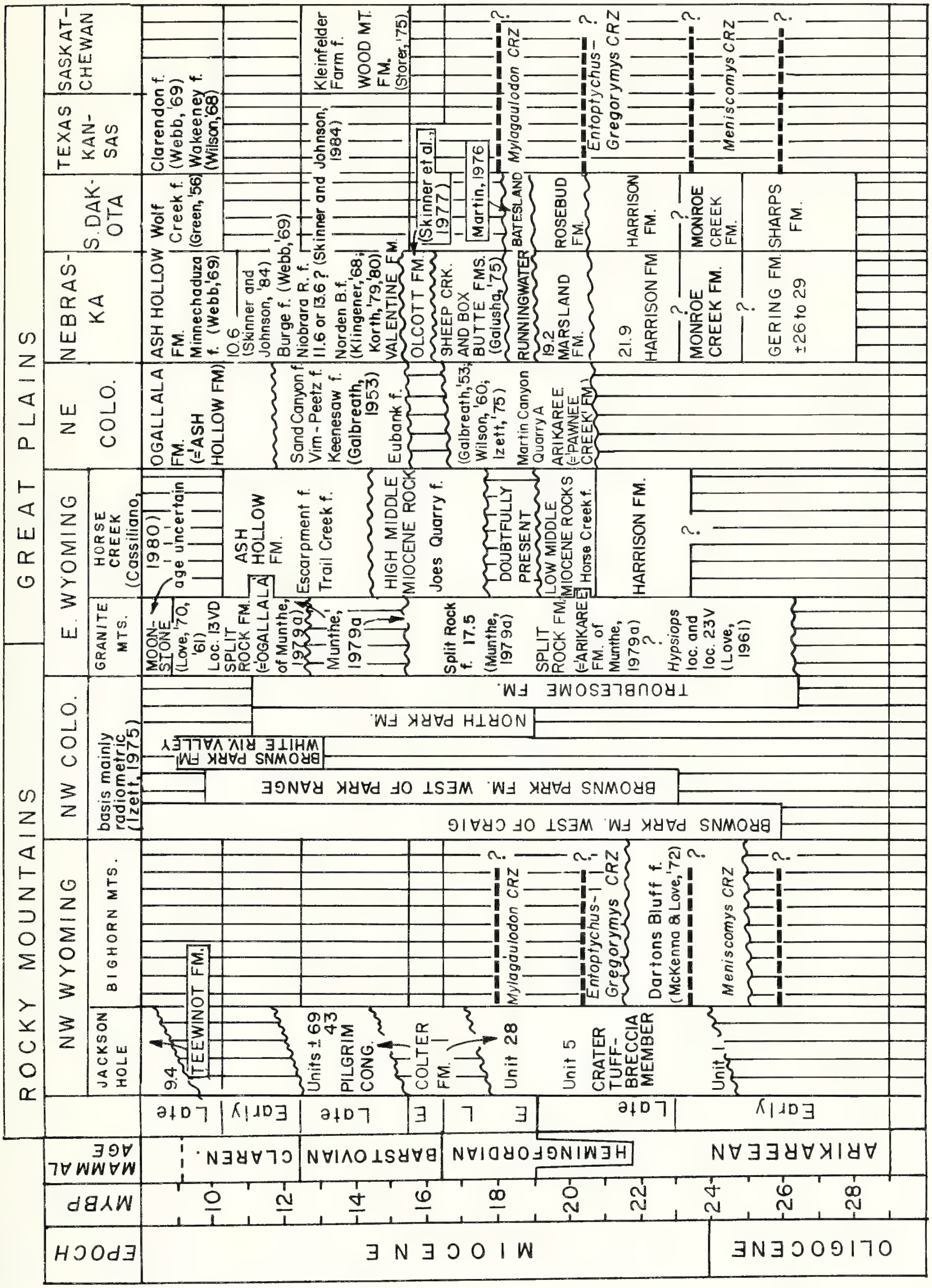

Fig. 29.—Biostratigraphic correlation of the Colter Formation and faunas with rocks and faunas of the Great Plains and Rocky Mountains. See Fig. 28 for further explanation.

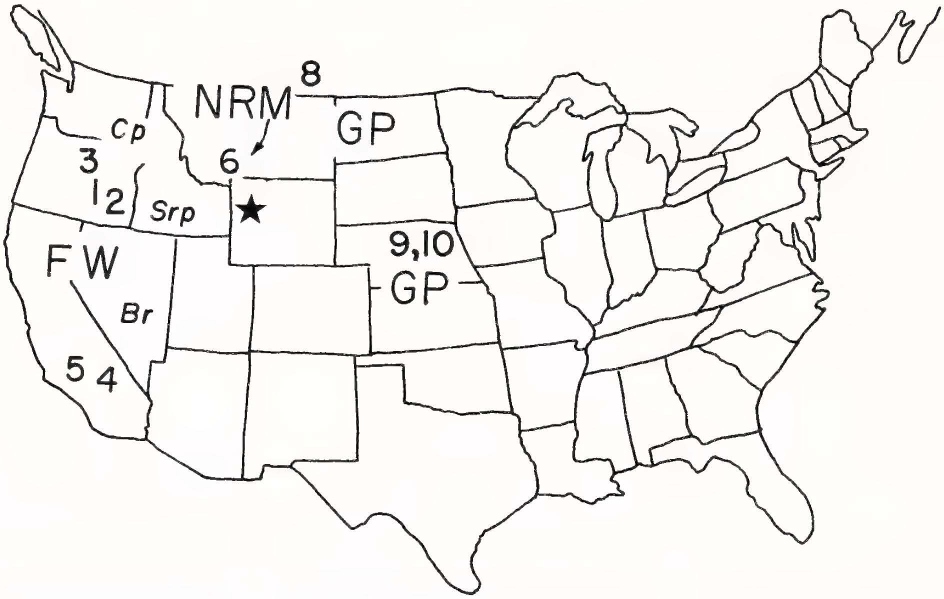

Fig. 30.—Location of Barstovian sites with diverse mammal faunas. *Far West* (FW): 1, Red Basin (Shotwell, 1968). 2, Quartz Basin (Shotwell, 1968). 3, Mascall (Downs, 1956). 4, Barstow (Lindsay, 1972). 5, Dome Spring (James, 1963). Cp, Columbia Plateau. Srp, Snake River Plain. Br, Basin and Range. *Northern Rocky Mountains* (NRM): *, Jackson Hole (see Fig. 1 for enlargement). 6, Anceney (Dorr, 1956; Sutton, 1977). *Great Plains* (GP): 8, Kleinfelder Farm (Storer, 1975). 9, Norden Bridge (Klingener, 1968) and "Niobrara River" (Webb, 1969). 10, Annies Geese Cross Quarry (Korth, 1979, 1980).

graphic regions from which diverse small-mammal assemblages are known—The Far West (including the Columbia Plateau, Snake River Plain, Basin and Range, and West Coast), the Northern Rocky Mountains (mountainous areas of Wyoming and Montana), and the Great Plains (plains east of the Rockies in Colorado, Wyoming, Nebraska, South Dakota, and Saskatchewan) (Fig. 30). At least 11 genera range throughout these geographic regions (Fig. 31). The faunal continuity suggests that genera listed in Fig. 31 can be regarded as characteristic of the late Barstovian. All but *Diprionomys, Spermophilus,* and *Scalopoides* are known from the upper member of the Barstow Formation (Lindsay, 1972), strata that Wood et al. (1941) considered to yield faunas typical of Barstovian land-mammal age.

Two genera and three species that occur in Jackson Hole (Fig. 32) are known from the Great Plains but have never been reported from the Far West. One genus and two species, however, show the opposite relationship—they are known from Jackson Hole and the Far West, but not from the Great Plains (Fig. 32). The presence of more Great Plains than western taxa in the Cunningham Hill Fauna may imply greater affinity with eastern faunas, but the differences are not statistically significant. The intermingling of eastern and western taxa at Jackson Hole, the geographically intermediate site, seems to reflect a gradual west to east change in taxonomic composition of Barstovian faunas. Factors that limited distribution, such as distance, vegetation, physiographic barriers, climate, and competition were apparently affecting individual genera and species rather than entire communities.

The overlap of taxa at Jackson Hole (Fig. 32) leads to the conclusion that the Great Plains faunas that contain *Shaubeumys, Diprionomys agrarius, Copemys kelloggae, Domninoides storeri,* and low crowned species of *Lignimus* correlate with Far West faunas that lack those taxa but include *Mojavemys, Pseudotheridomys pagei,* and *Tamias ateles.* Therefore, faunas at the Norden Bridge and Annies Geese Cross Quarries of the Nebraska Great Plains, considered as "Valentinian" provincial age in the terminology of Schultz et al. (1970, and references therein) probably correlate with the typical late Barstovian faunas of the upper Barstow Formation (Lindsay, 1972). The shared presence of *Cupidinimus, Copemys,* and *Perognathus* at these sites is consistent with this hypothesis. The step-wise correlation to the type locality at Barstow suggests that Norden Bridge and Annies Geese Cross quarries are late Barstovian in age. If so, the lower part of the "Valentinian" provincial age overlaps the late Bar-

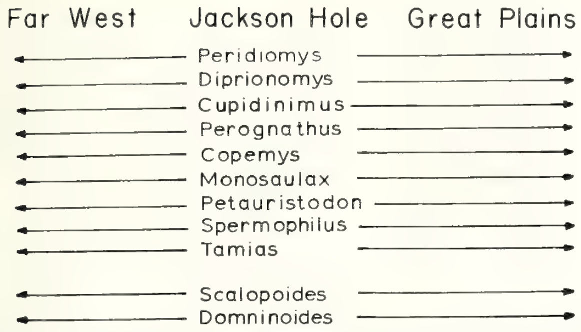

Fig. 31.—Genera that characterize late Barstovian faunas throughout the western United States and southern Saskatchewan.

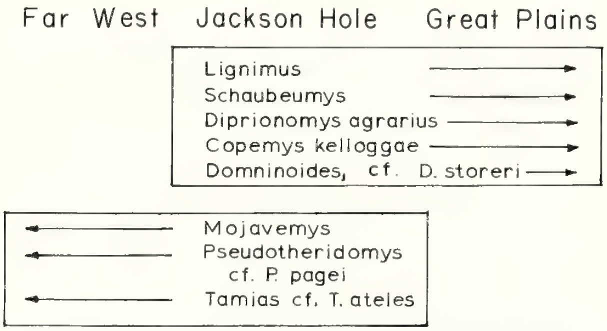

Fig. 32.—Late Barstovian mammals found together at Jackson Hole but usually restricted to either the Far West or Great Plains.

stovian. Because of this apparent redundancy, the term "Valentinian" is not included on any of the correlation charts.

At least 13 late Barstovian species are found only in Far West faunas, five species are known only from Jackson Hole, and six species are known only from the Great Plains (Table 21). Different ecologic settings in each of the three regions provides the most likely explanation for the three assemblages of species. Wide geographic separation would help to maintain the differences. Distinctive assemblages of Far West, Rocky Mountain, and Great Plains species also characterize modern small-mammal faunas (Hall, 1981). The different modern assemblages coincide with differences in physiography, vegetation, and climate (Trewartha et al., 1968:maps 1, 2, 3, 9). Physiographic differences between the three areas had already developed by the Eocene with uplift of the Rocky Mountains (Love, 1960). During the Hemingfordian and Barstovian, renewed tectonism in the northern Rockies delineated the modern basins and ranges (Rasmussen, 1973; Thompson et al., 1981; Fields et al., 1985). It is, therefore, likely that by the late Barstovian, the Rocky Mountains were prominent highlands that were ecologically separated from the Far West and Great Plains. Ecological separation, as is evident today, would have resulted from differences in vegetation and climate that accompany differences in altitude and distance from oceans.

Paleofloral data provide some independent evidence that the ecologic setting of the Rocky Mountains differed from that of areas to the west and east by Barstovian time. Leopold and MacGinitie (1972: 186) concluded that floras of the Rockies, among them a pollen flora from the lower Colter Formation, were distinct from those of the Far West and eastern U.S. by the middle Eocene. They provided floral lists for the Beaverhead Basin flora (late Oligocene, Montana), Split Rock Formation (Hemingfordian, Wyoming), Trapper Creek flora (mid?-Miocene, Idaho), Moonstone Formation (late Miocene, Wyoming), and Teewinot Formation (Hemphillian, Jackson Hole) that imply coniferous vegetation of continental aspect has grown in the Rockies since the mid-Tertiary. A study of fossil pollen from the Teewinot Formation showed that essentially modern vegetation had arrived in Jackson Hole by the early Hemphillian (C. Barnosky, 1984). In contrast to vegetation of the Rocky Mountains, temperate conifers and broad-leaved deciduous plants were common in Washington, Oregon, Nevada, and northcentral California from at least Arikareean (late Oligocene/early Miocene) to Hemphillian (late Miocene) time (Wolfe, 1969). Vegetation in the Great Plains was more diverse than in the Rockies and related strongly to present Appalachian plants, as evidenced by the late Miocene Kilgore Flora of Nebraska (MacGinitie, 1962; Leopold and MacGinitie, 1972:163).

Table 21.—*Species confined to one geographic area.*

Far West:	*Mojavemys lophatus, Mojavemys mascallensis, Mojavemys alexandrae, Cupidinimus halli, Cupidinimus "nebraskensis," Cupidinimus eurekensis, Perognathus minutus, Copemys longidens, Copemys esmeraldensis, Copemys russelli, Copemys tenuis, Copemys barstowensis, Copemys dentalis*
Jackson Hole:	*Lignimus transversus,* new species, *Mojavemys magnumarcus,* new species, *Cupidinimus* sp., *Spermophilus* near *S. primitivus, Oreolagus colteri,* new species
Great Plains:	*Lignimus montis, Lignimus* cf. *L. hibbardi, Cupidinimus nebraskensis, Perognathus trojectioansrum, Copemys niobrariensis, Russellagus vonhofi*

Temporal differences between sites of the three geographic regions cannot be discounted, but do not provide the simplest explanation for the geographic restriction of species (Table 21). Related species in the different regions are at a similar evolutionary grade, which would not be expected if morphologic differences were due mainly to temporal isolation. Very low crowned species of *Lignimus* occur at Jackson Hole (*L. transversus*), Kleinfelder Farm (*L. montis*), and Norden Bridge (*L.* cf. *L. montis*). Low crowned species of *Cupidinimus* are present at Barstow (*C.* "*nebraskensis*"), Anceney (*C. madisonensis*), Annies Geese Cross Quarry, and Norden Bridge (*C. nebraskensis*). High crowned species of *Mojavemys* with enamel chevrons on upper teeth are present at Jackson Hole (*M. magnumarcus*) and Barstow (*M. lophatus*).

Preservation or collection bias is probably even less important in accounting for the differences between Barstovian species of the three regions (Table 21). The same genera occur in most sites, and the same species are present in some (Figs. 27, 31, 32). Collection bias probably does influence the number of species known to be restricted to one geographic region. The region with the most sites, the Far West, also has the greatest number of restricted species, 13. That with the fewest sites, Jackson Hole, also has the fewest restricted species, 5.

The few fossils from the East Pilgrim and Emerald Lake faunas prevent any detailed statements about their affinities, but some facts are suggestive. *Merycochoerus proprius magnus* and *Parahippus tyleri* are otherwise known only from Nebraska (both) and northeast Colorado (*M. proprius magnus*). *Merychyus arenarum* is known mainly from Nebraska and eastern Wyoming. Presence of these taxa in the East Pilgrim Fauna implies at least some faunal continuity between Jackson Hole and the Great Plains during the early Hemingfordian.

In the Emerald Lake Fauna three of the four species are new, which is consistent with a postulate of distinct ecologic settings in the Rocky Mountains as far back as the Arikareean. One genus, *Niglarodon,* is known only from the Rocky Mountains and possibly the Great Plains (Rensberger, 1981). *Allomys cristabrevis* is closely related to a Great Plains allomyine rodent, *A. harkseni. A. cristabrevis* and *Niglarodon* sp. suggest faunal affinity with the Great Plains. *Desmatochoerus leidyi* provides the only evidence for an overlapping range of a western taxon.

CONCLUSIONS

1. Thirty-two species of mammals are now known from the Colter Formation.

2. Three distinct faunal assemblages are recognized. They are designated the Emerald Lake Fauna, the East Pilgrim Assemblage, and the Cunningham Hill Fauna.

3. The Emerald Lake Fauna most resembles those of the upper half of the *Meniscomys* Concurrent-range Zone (late–early Arikareean).

4. The East Pilgrim Assemblage includes three stratigraphically separated local faunas. The uppermost one, the Unit 28 local fauna, yields species that also are present in the Runningwater Formation (early Hemingfordian). However, the stratigraphically lowest, the Unit 5 local fauna, is represented only by *Merychyus arenarum,* an oreodont that is known otherwise only from the Marsland Formation and rocks equivalent in age to the Marsland (late Arikareean).

5. The Cunningham Hill Fauna is late Barstovian in age and contains taxa that occur only in the *Copemys longidens* and *Copemys russelli* Assemblage zones of the Barstow Formation.

6. Faunal similarities suggest that the oldest bed in the Colter Formation (Unit 1SR) correlates with parts of the John Day (Oregon), Deep River (Montana), and Monroe Creek (South Dakota) Formations, the Cabbage Patch beds (Montana), and with deposits containing the Peterson Creek fauna (Idaho).

7. Tuff near the top of the Crater Tuff-breccia Member (Unit 28) correlates most closely with the Runningwater Formation (Nebraska) because *Parahippus tyleri* and *Merycochoerus proprius magnus* are present.

8. On the basis of directly comparable faunas, the Pilgrim Conglomerate Member (Units 43 and O) correlates with parts of the Barstow (California), Caliente (California), Deer Butte (Oregon), Madison Valley (Montana), and Wood Mountain (Saskatchewan) Formations and the Butte Creek Volcanic Sandstone (Oregon).

9. The Emerald Lake Fauna (Unit 1SR) is about 23.6 to 24.6 my old, the East Pilgrim Assemblage (Units 5 to 28) between 18 and 20 my old, and the Cunningham Hill Fauna (Units 0 to 43) about 12

to 14 my old, based on correlations of the faunal ages with the radiometric scale.

10. *Lignimus, Schaubeumys, Diprionomys agrarius, Copemys kelloggae, Domninoides* cf. *D. storeri, Mojavemys, Pseudotheridomys* cf. *P. pagei,* and *Tamias* cf. *T. ateles* occur contemporaneously in Jackson Hole. The last three are otherwise reported only from the Far West, and the rest only from the Great Plains.

11. The association mentioned above helps to establish a step-wise correlation that suggests early "Valentinian" and late Barstovian refer to overlapping intervals of time.

12. The late Barstovian and Arikareean faunas in Jackson Hole contain suites of species that differ from those of late Barstovian and Arikareean faunas of the Far West and Great Plains. The differences in species are mainly attributed to ecological differences that arise from physiographic, vegetational, and climatic differences between the geographically separated sites.

13. Miocene faunas in Jackson Hole show greater affinity with Great Plains faunas with those of the Far West.

14. New Barstovian species include (Cunningham Hill Fauna): *Oreolagus colteri,* new species (ochotonid), *Lignimus transversus,* new species, and *Mojavemys magnumarcus,* new species (geomyids), as well as a new species of *Cupidinimus* (heteromyid) that is named and described elsewhere. *O. colteri* possesses root bumps on the upper cheek teeth as a primitive feature, but is advanced in the short anteroloph of P^3. *L. transversus* is very low crowned, like *L. montis. M. magnumarcus* is high crowned and possesses enamel chevrons on upper molars. The most similar species in these respects is *M. lophatus.*

15. New Arikareean species include (Emerald Lake Fauna): *Allomys cristabrevis,* new species (aplodontid), and *Archaeolagus emeraldensis,* new species (leporid). *A. cristabrevis* is slightly more primitive than *A. harkseni* in elongation of internal crests, but otherwise is similar. *A. emeraldensis* most closely resembles *A. ennisianus* in intermediate size and the relatively elongate P_3.

16. The late Barstovian Cunningham Hill Fauna yields the first records of the following taxa in the northern Rocky Mountains: *Petauristodon, Diprionomys agrarius, Lignimus, Mojavemys, Copemys kelloggae, Schaubeumys.*

17. The Hemingfordian East Pilgrim 5 local fauna extends the range of *Merycochoerus proprius magnus* and *Parahippus tyleri* from the Great Plains into the northern Rocky Mountains.

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CAPTIONS FOR PLATES

Plate I.—Screen-washing localities in the Colter Formation. *Top:* Cunningham Hill, UWBM loc. C0236. Bones weather from small channel. Arrow points to hammer for scale. *Bottom:* Man's left foot on North Pilgrim 2, UWBM loc. C0237. Bones erode from scarp to his left.

Plate II.—Teeth of *Domninoides* cf. *D. storeri, Allomys cristabrevis,* new species, *Diprionomys agrarius, Spermophilus* near *S. primitivus,* and *Petauristodon* from Colter Formation. Anterior at top for occlusal views. A, *Domninoides* cf. *D. storeri,* UWBM 62728, M_3, loc. C0237, occlusal view, stereo pair. B, same as A, lingual view, anterior at left. C, *Allomys cristabrevis,* new species, holotype, AMNH 89727, M_1, UWBM loc. C0241, occlusal view. D, *Diprionomys agragrius,* UWBM 62631, M^1 or M^2, loc. C0237, occlusal view, stereo pair. E, *D. agrarius,* UWBM 62671, M_1 or M_2, loc. C0237, occlusal view, stereo pair. F, *D. agrarius,* UWBM 62660, P_4, loc. C0237, occlusal view. G, same as D, lingual view, anterior at right. H, same as E, labial view, anterior at right. I, same as F, labial view, anterior at left. J, *Spermophilus* near *S. primitivus,* UWBM 62739, M_1 or M_2, loc. C0237, occlusal view, stereo pair. K, *S.* near *S. primitivus,* UWBM 62741, M_3, loc. C0237, occlusal view, stero pair. L, *S.* near *S. primitivus,* UWBM 62733, M_1 or M_2, loc. C0237, occlusal view, stereo pair. M, *Petauristodon,* species indeterminate, UWBM 62743, M_3, loc. C0237, occlusal view, stereo pair. Scale bars equal 1 mm.

Plate III.—Teeth of lagomorphs from Colter Formation. A, *Oreolagus colteri,* new species, UWBM 62704, P^4 or M^1, loc. C0237, occlusal view, stereo pair, labial at top. B, *O. colteri,* new species, holotype, UWBM 62698, P^4 or M^1, from UWBM loc. C0237, occlusal view, stereo pair, labial at top. C, *O. colteri,* new species, UWBM 62720, P^4 or M^1, loc. C0237, anterior view, labial at left. D, same as A, labial view, anterior at right. E, same as B, labial view, anterior at right. F, *O. colteri,* new species, UWBM 62693, P^3, loc. C0237, occlusal view, stereo pair, labial at top. G, same as C, occlusal view, stereo pair, anterior at left, labial at top. H, *O. colteri,* new species, UWBM 62714, M^2, loc. C0237, occlusal view, anterior at left. I, *Archaeolagus emeraldensis,* new species, AMNH 89801, P_4–M_2, from UWBM loc. C0241, occlusal view, stereo pair, anterior at top. J, *O. colteri,* new species, UWBM 62697, broken DP_3 (anterior two-thirds), loc. C0237, occlusal view, stereo pair, lingual at top. K, *Archaeolagus emeraldensis,* new species, holotype, P_3, loc. C0241, occlusal view, stereo pair, anterior at top. Scale bars equal 1 mm.

Plate IV.—Teeth of *Cupidinimus* and *Peridiomys* from Colter Formation. Anterior at top for occlusal views. A, *Cupidinimus* sp., UWBM 62798, P_4, loc. C0236, labial view, anterior at left. B, Same as A, occlusal view, stereo pair. C, *C.* sp., UWBM 62807, M_1, loc. C0236, occlusal view, stereo pair. D, *C.* sp., UWBM 62788, P^4, loc. C0236, occlusal view, stereo pair. E, *C.* sp., UWBM 62806, M^1, loc. C0236, occlusal view, stereo pair. F, *C.* sp., UWBM 62809, M_2, loc. C0236, occlusal view, stereo pair. G, *C.* sp., UWBM 62802, M^2, loc. C0236, occlusal view, stereo pair. H, same as D, anterior view, labial at right. I, same as C, labial view, anterior at left. J, same as F, labial view, anterior at left. K, same as E, lingual view, anterior at right. L, same as G, lingual view, anterior at left. M, *Peridiomys* sp., UWBM 62664, M_1 or M_2, loc. C0237, labial view, anterior at left. N, same as M, occlusal view. O, *P.* sp., UWBM 62638, M^1 or M^2, loc. C0236, occlusal view, stereo pair. P, same as O, lingual view, anterior at left.

Plate V.—Teeth of *Lignimus transversus,* new species, from Colter Formation. Anterior at top for occlusal views. A, UWBM 62655, P_4, loc. C0237, labial view, anterior at left. B, same as A, occlusal view, stereo pair. C, UWBM 62662, holotype, M_1, loc. C0237, occlusal view, stereo pair. D, UWBM 62663, M_1, loc. C0237, occlusal view, stereo pair. E, UWBM 62666, M_1 or M_2, loc. C0237, occlusal view, stereo pair. F,

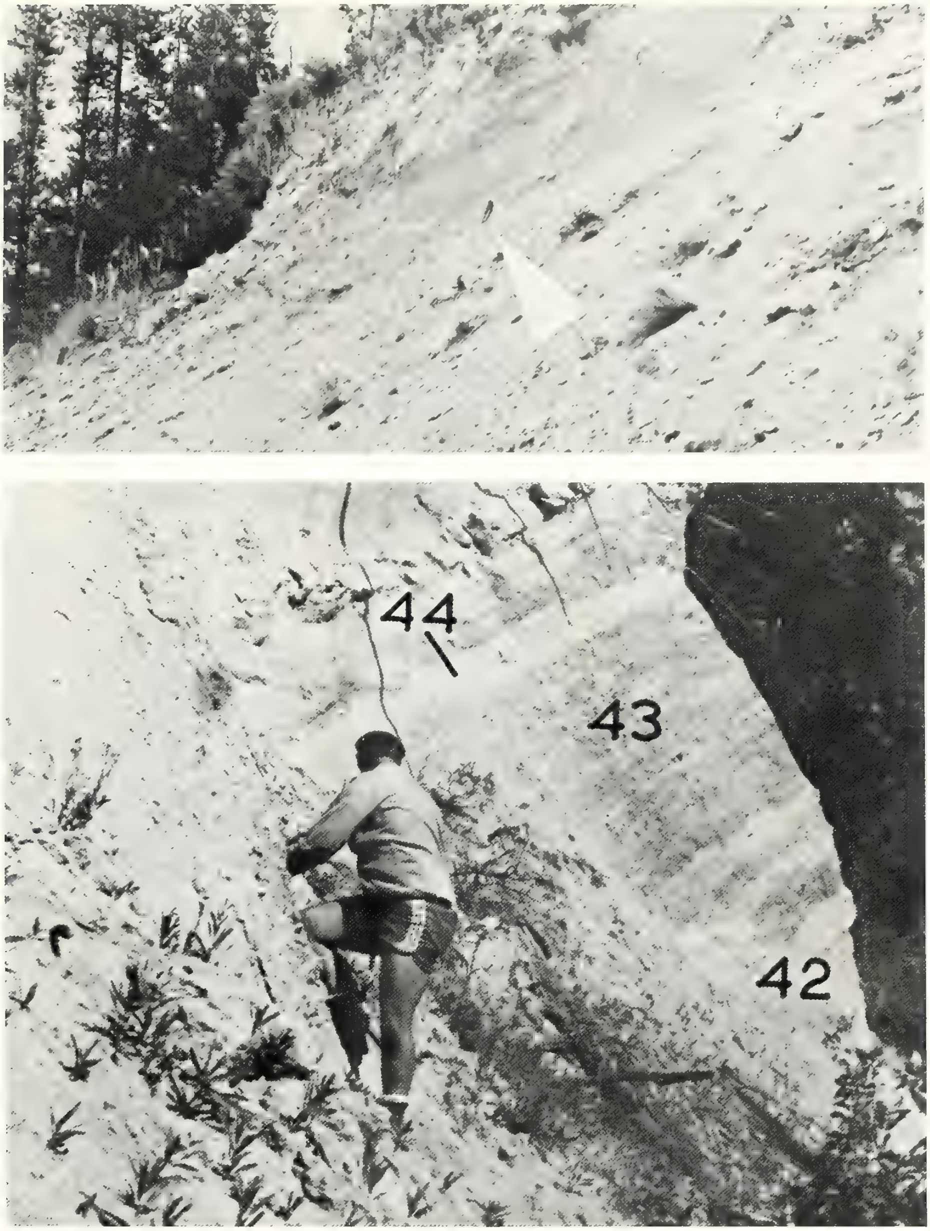
same as D, labial view, anterior at right. G, same as C, labial view, anterior at right. H, same as E, labial view, anterior at right. I, UWBM 62687, M_3, loc. C0237, labial view, anterior at right. J, same as I, occlusal view. K, UWBM 62759, P^4, loc. C0236, occlusal view. L, same as K, anterior view, labial at left. M, UWBM 62777, M^1, loc. C0236, occlusal view, stereo pair. N, same as M, lingual view, anterior at right. O, UWBM 62616, P^4, loc. C0237, occlusal view. P, same as O, anterior view, labial at right. Q, UWBM 62634, M^1 or M^2, loc. C0237, occlusal view, stereo pair. R, same as Q, lingual view, anterior at right. S, UWBM 62645, M^3, loc. C0237, occlusal view. T, same as S, lingual view, anterior at right. U, UWBM 62621, M^1 or M^2, from loc. C0237, lingual view, anterior at right. V, same as U, occlusal view.

Plate VI.—Teeth of *Mojavemys magnumarcus,* new species, from Colter Formation. Anterior at top for occlusal views. A, UWBM 62795, P_4, loc. C0236, occlusal view, stereo pair. B, UWBM 62780, M_1, loc. C0236, occlusal view. C, same as A, labial view, anterior at right. D, UWBM 62766, M_2, loc. C0236, occlusal view, stereo pair. E, KUVP 17493, M_3, loc. C0236, occlusal view, stereo pair. F, same as B, labial view, anterior at left. G, UWBM 62784, M_1, loc. C0236, occlusal view. H, UWBM 62783, M_2, loc. C0236, occlusal view, stereo pair. I, UWBM 62770, M_1, loc. C0236, occlusal view. J, same as D, labial view, anterior at left. K, same as G, labial view, anterior at left. L, same as H, labial view, anterior at right. M, same as I, labial view, anterior at right. N, same as E, labial view, anterior at left. O, UWBM 62617, P^4, loc. C0237, occlusal view, stereo pair. P, same as O, anterior view, labial at left. Q, UWBM 62641, holotype, M^1 or M^2, loc. C0237, occlusal view. R, KUVP 17498, M^3, loc. C0236, occlusal view, stereo pair. S, same as R, lingual view, anterior at right. T, same as Q, lingual view, anterior at right.

Plate VII.—Teeth of *Copemys kelloggae, Pseudotheridomys* cf. *P. pagei, Parahippus tyleri,* and *Merychippus* from Colter Formation. A, *Copemys kelloggae,* UWBM 62821, M^1–M^3, loc. C0236, occlusal view, stereo pair, anterior at top. B, *C. kelloggae,* UWBM 62819, M_1, loc. C0236, occlusal view, stereo pair, anterior at top. C, *Pseudotheridomys* cf. *P. pagei,* KUVP 17486, P^4 or M^1, loc. C0236, occlusal view, stereo pair, anterior at top. D, *Parahippus tyleri,* CMNH 21617b, P_3–M_3, loc. C0240, occlusal view, anterior at left. E, *Merychippus,* species indeterminate, KUVP 40359c, lower P or M, loc. C0236, occlusal view, anterior at right. F, same as D, labial view. G, same as E, labial view. H, *Parahippus tyleri,* CMNH 21617a, upper cheek teeth, loc. C0240, occlusal view, anterior at left. I, same as H, labial view, anterior at left. Upper scale is for A–C; lower scale for D–G.

Plate VIII.—Oreodonts from Colter Formation. A, *Merychyus arenarum,* UWBM 63261, partial skull, loc. C0239, right lateral view, anterior at right. B, *Merycochoerus proprius magnus,* USNM 17919, anterior part of rostrum, loc. C0240, left lateral view, anterior at left. Diagrams at right show the dimensions measured for Tables 15, 17. Abbreviations: C, canine. I, incisor. IF, infraorbital canal. PM, premaxillary suture. PR, dorsal protrusion of premaxillary suture. NV, area of nasal vacuity. ROSLEN, rostrum length. Canine not preserved on side of specimen shown in B, but sketched on lower diagram to illustrate dimension C-M. Anterior end point for dimensions ROSLEN, PM at premaxilla-first incisor junction.

Plate IX.—*Desmatochoerus leidyi* from Colter Formation. A, AMNH 89724, skull, loc. C0241, left lateral view, anterior at left. B, same as A, posterior view. C, AMNH 89724, C_1–P_4, occlusal view, anterior at left.



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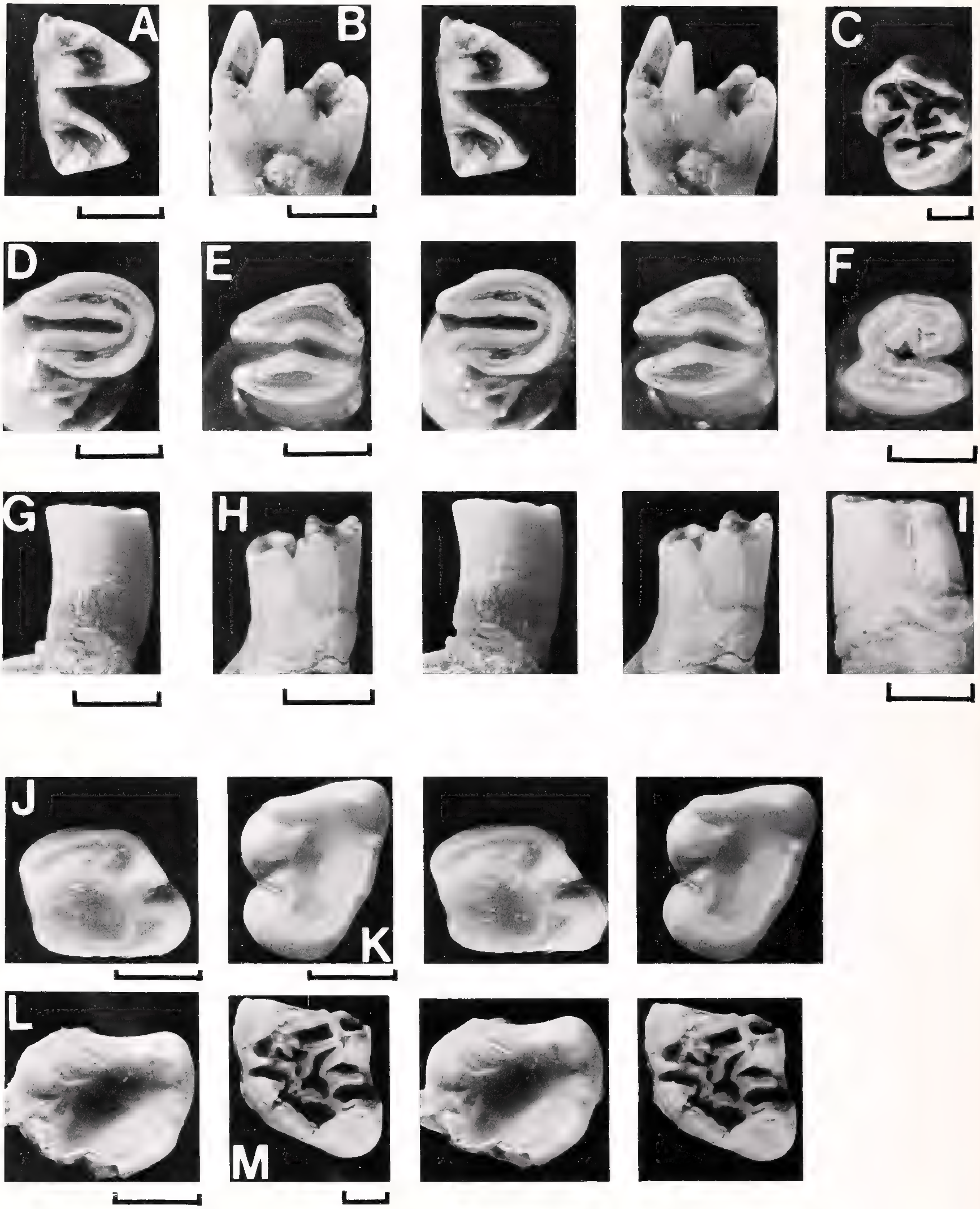

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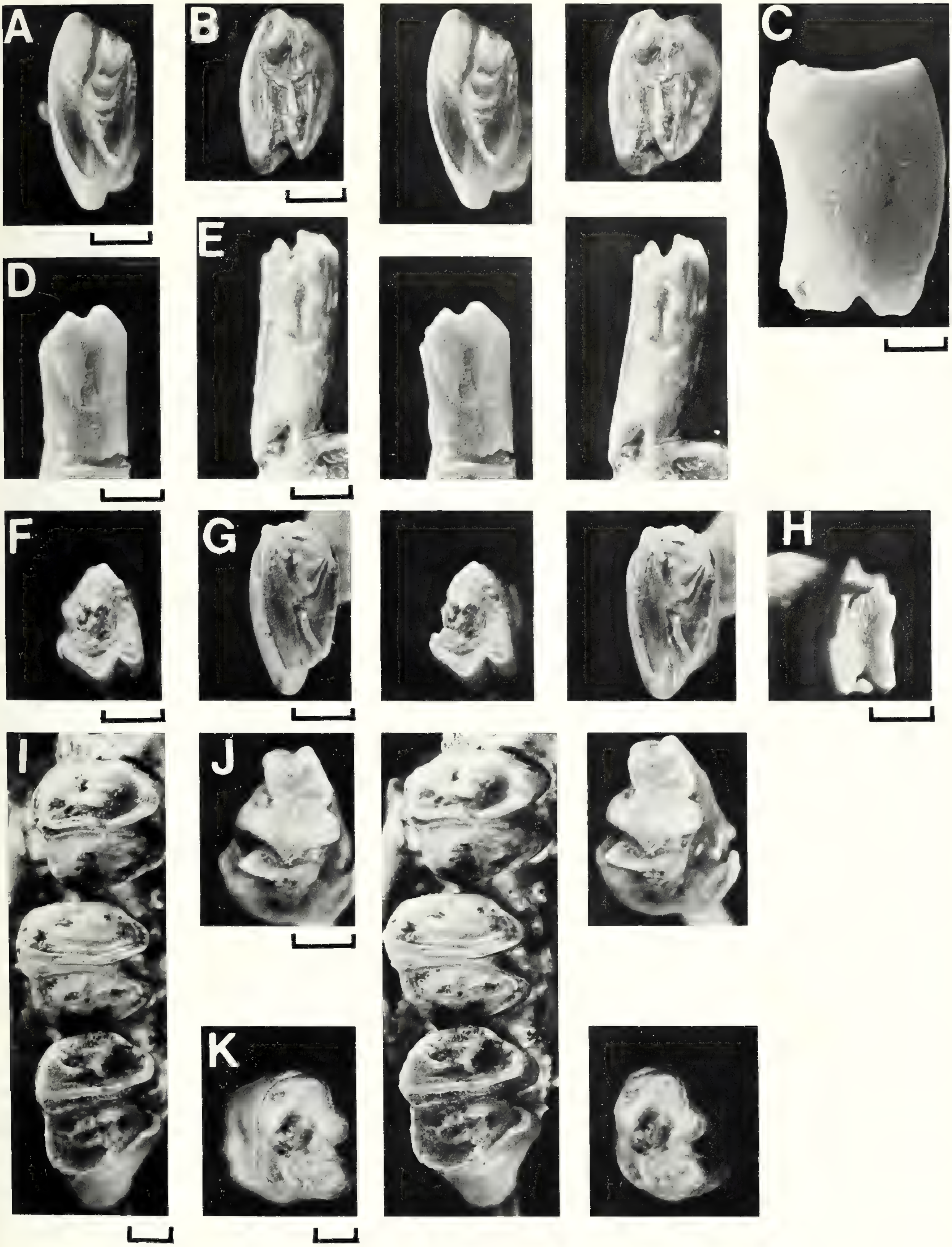

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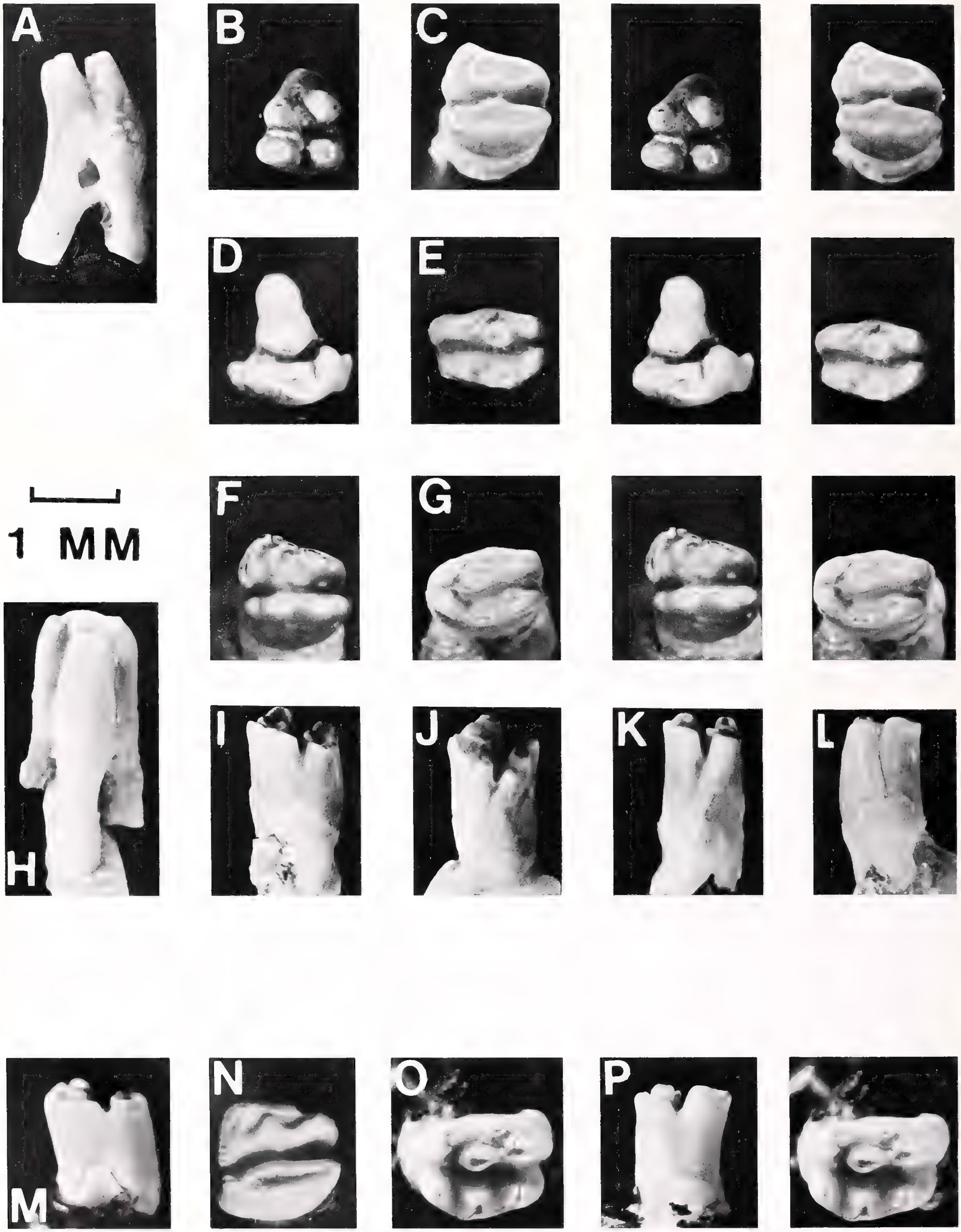

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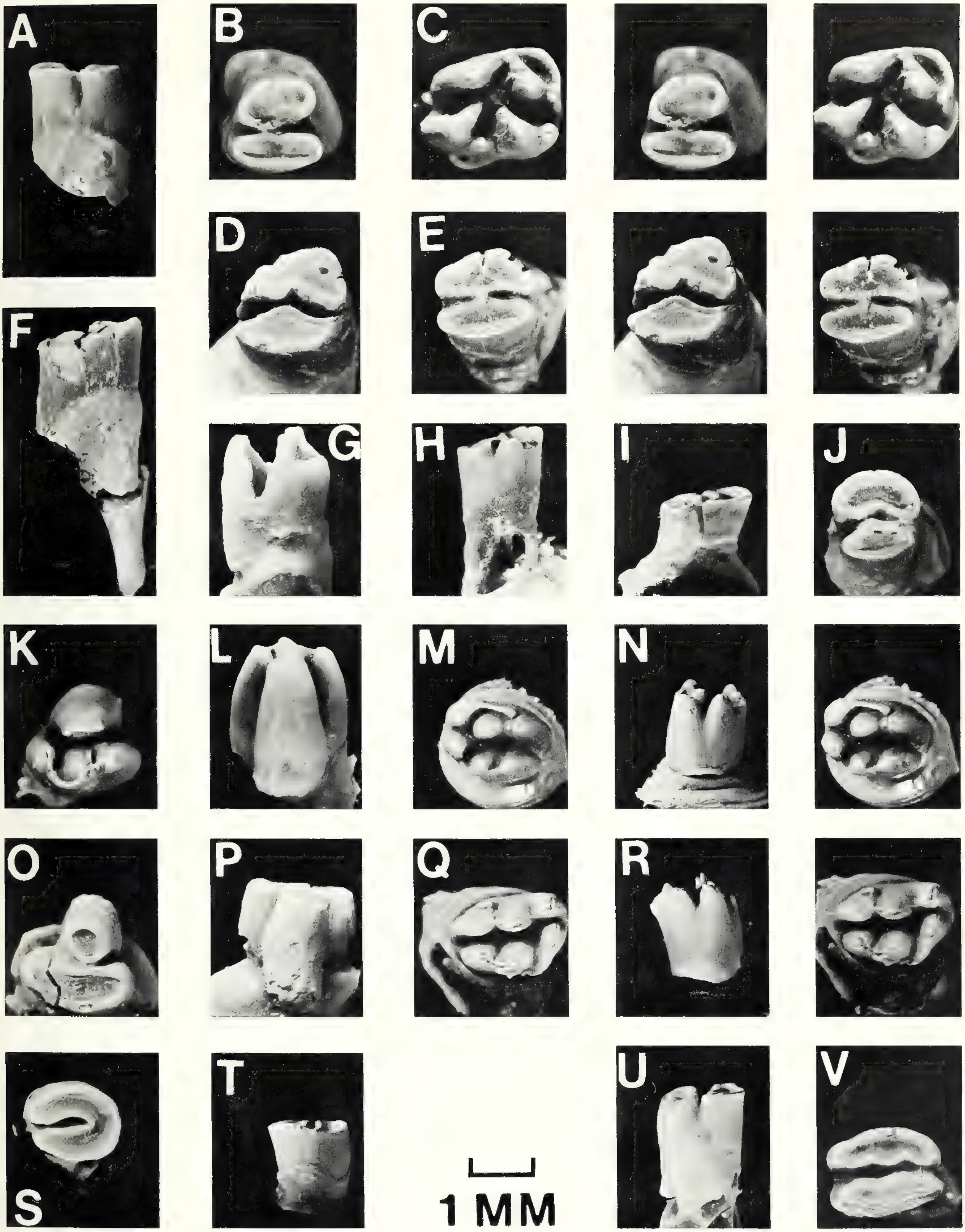

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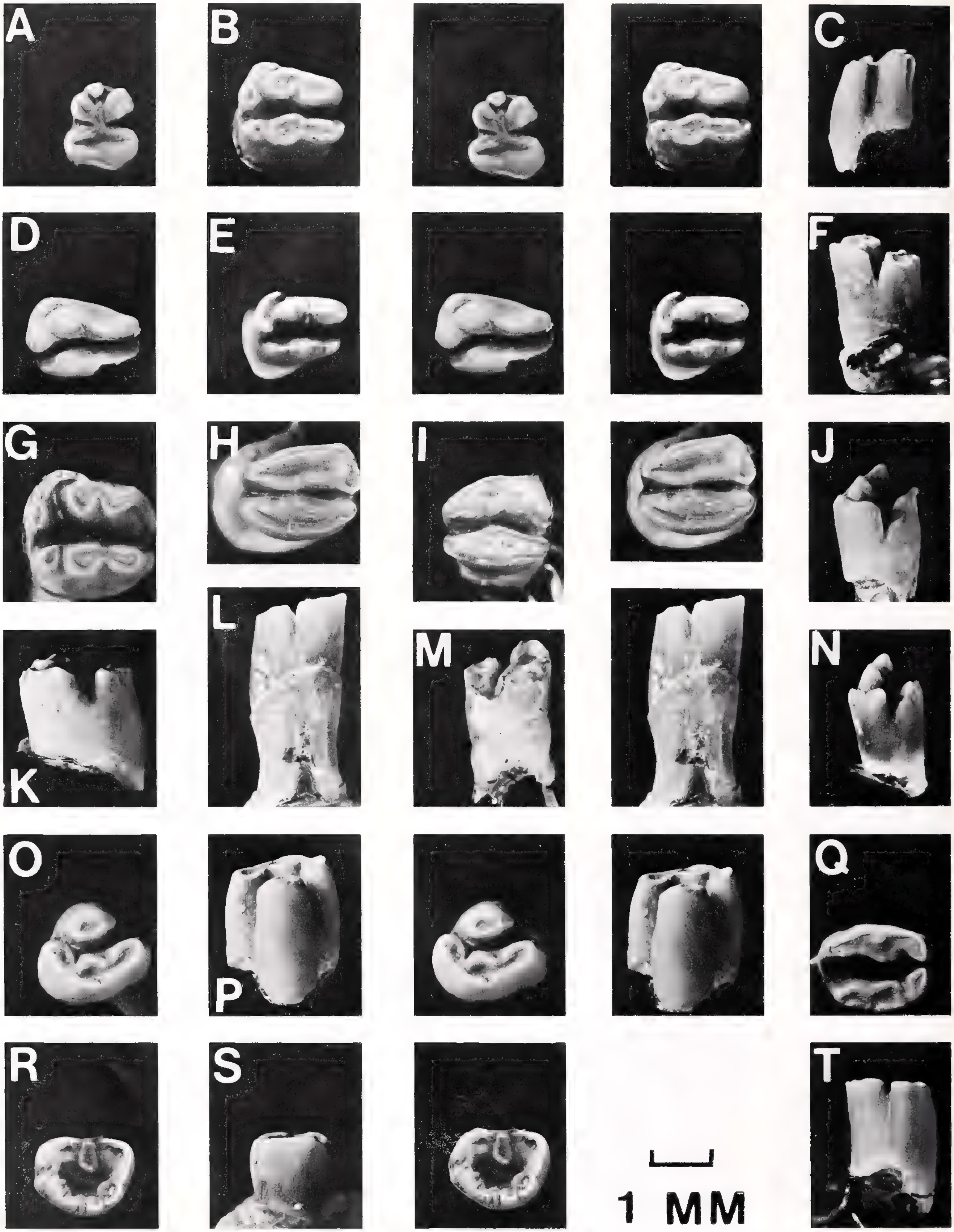

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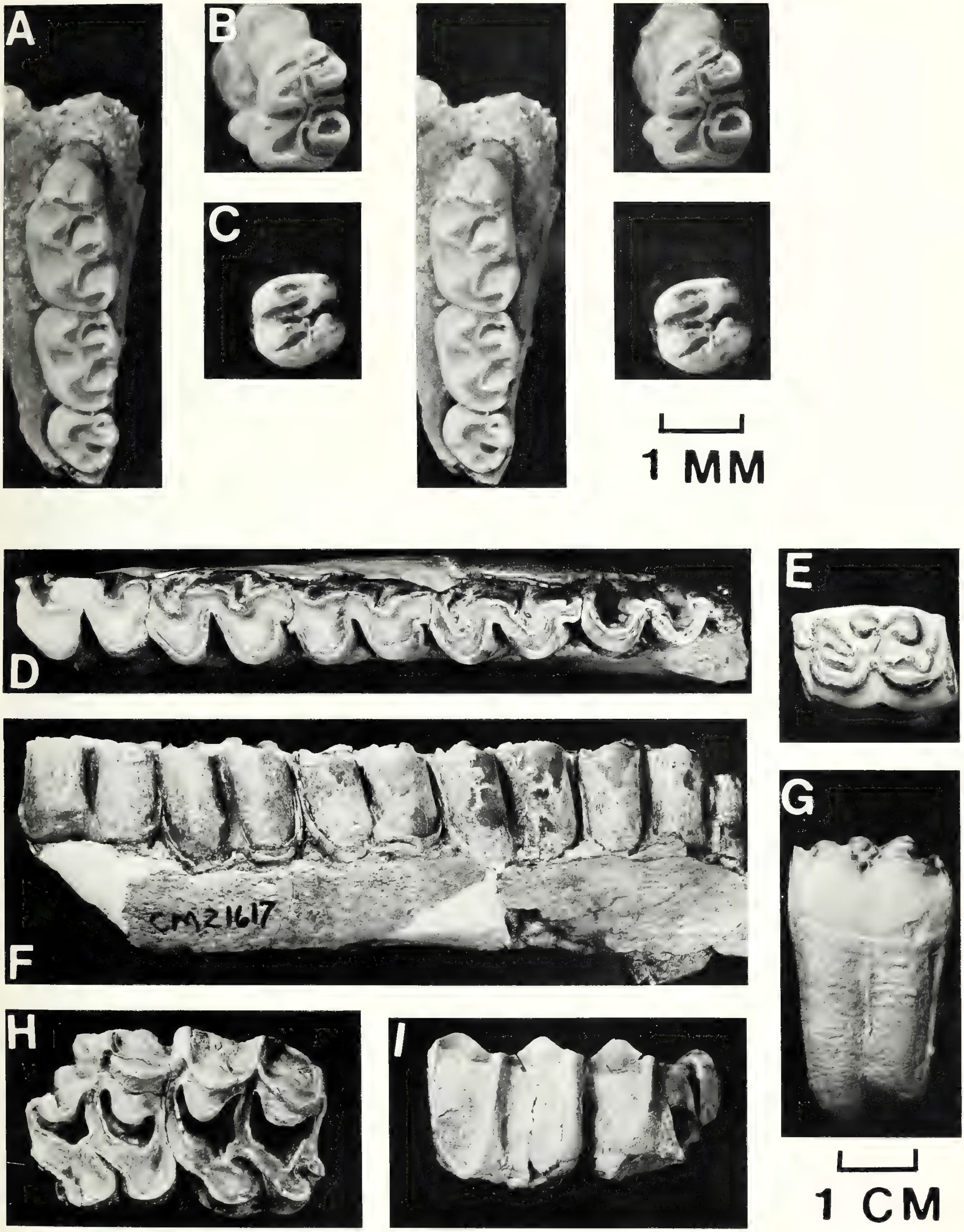

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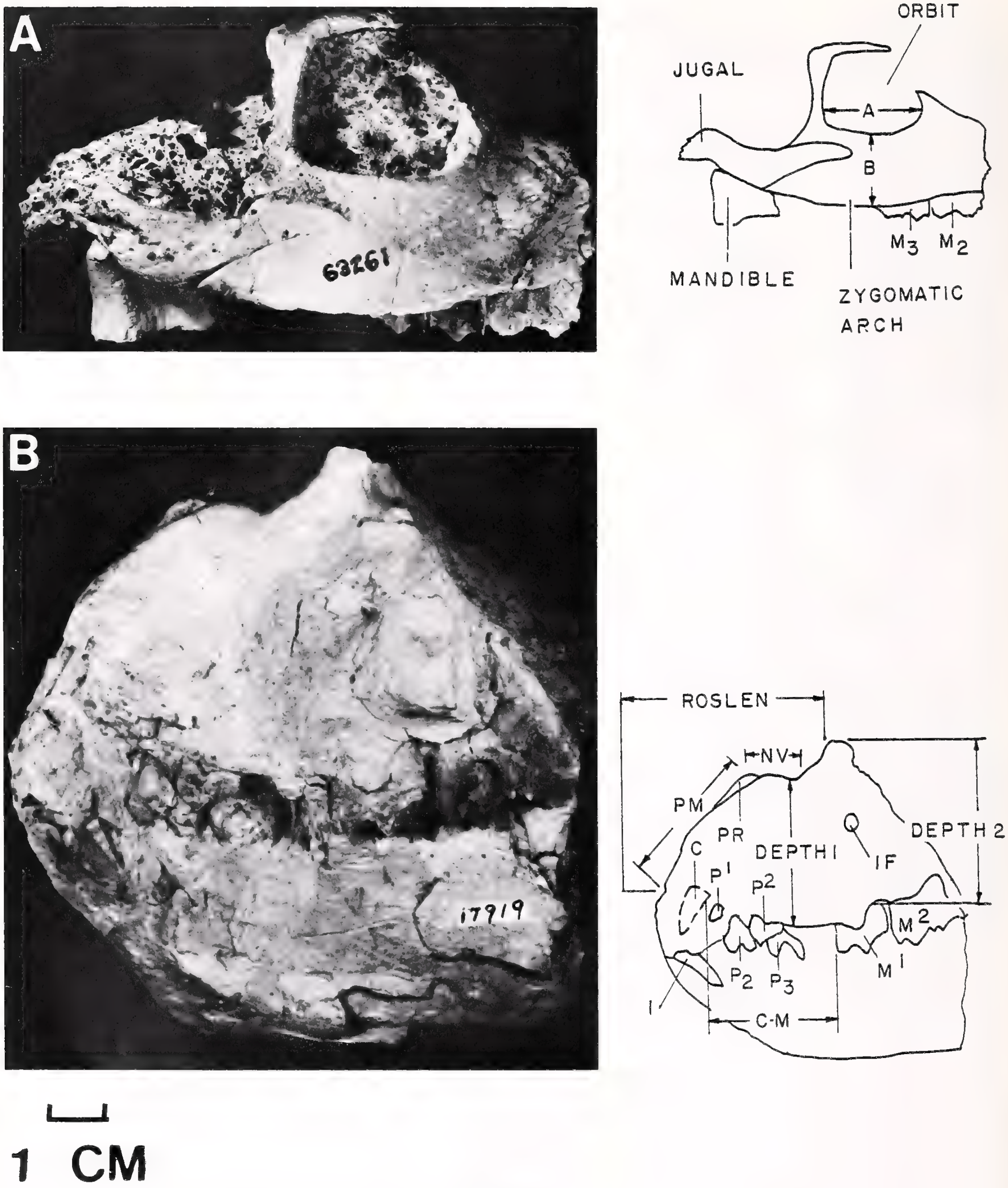
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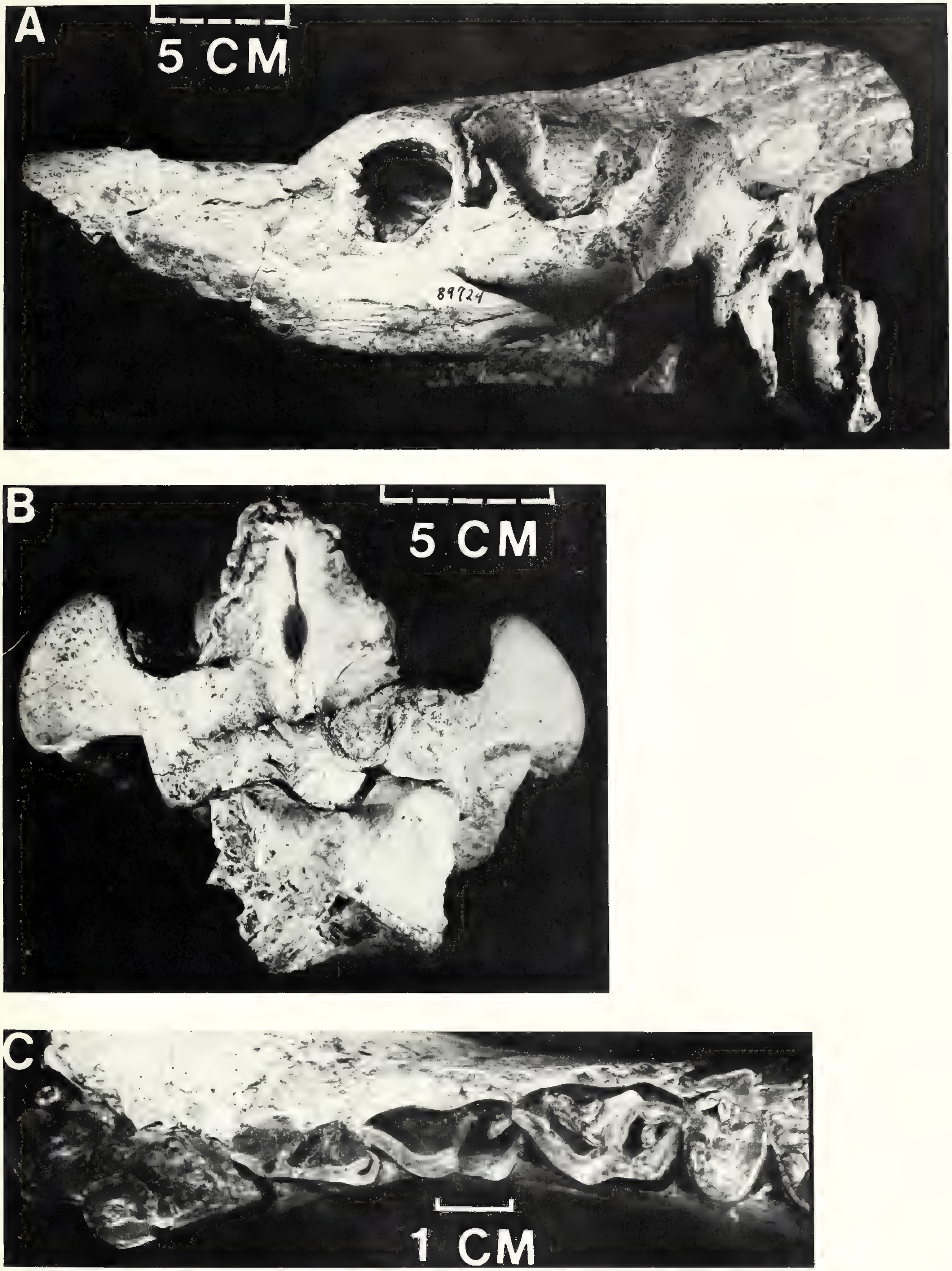

Plate IX

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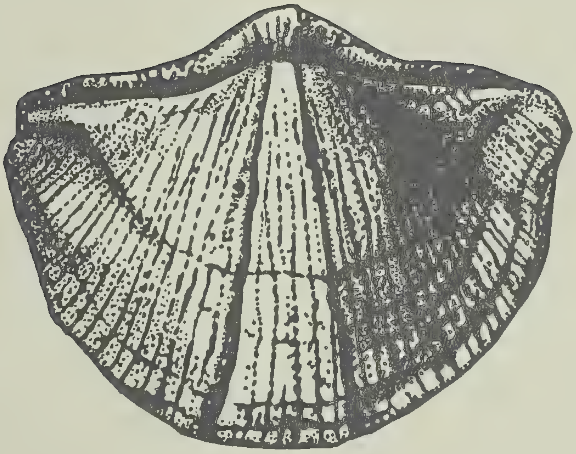

EARLY MISSISSIPPIAN BRACHIOPODS FROM THE GLEN PARK FORMATION OF ILLINOIS AND MISSOURI

JOHN L. CARTER

NUMBER 27 PITTSBURGH, 1988

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JOHN L. CARTER
Curator, Section of Invertebrate Fossils

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ABSTRACT

The Glen Park Formation of east-central Missouri and west-central Illinois contains a diverse brachiopod macrofauna consisting of 45 species assigned to 43 genera. New taxa proposed in this work include the new genera *Ruthiphiala,* type species *Productella sublaevis* Weller, 1914, a chonopectinine; and *Zeugopleura,* type species *Spirifer jeffersonensis* Weller, 1906, a syringothyrididine. New species are *Rhipidomella rockportensis* n. sp., *Schizophoria hortonensis* n. sp., *Schuchertella hardinensis* n. sp., *Subglobosochonetes jerseyensis* n. sp., *Rugosochonetes pikensis* n. sp., *Orbinaria? brownensis* n. sp., *Nigeroplica? illinoisensis* n. sp., *Argentiproductus auriculatus* n. sp., *Sentosia? ignota* n. sp., *Ovatia nascens* n. sp., *Shumardella fracta* n. sp., *Axiodeaneia glenparkensis* n. sp., *Rhynchopora prisca* n. sp., *Composita matutina* n. sp., *Cardiothyris pristina* n. sp., *Parallelora nupera* n. sp., *Unispirifer senex* n. sp., *Brachythyris hortonensis* n. sp., and *Eomartiniopsis kinderhookensis* n. sp.

The distribution of many short-ranging biostratigraphically useful brachiopod species in the Glen Park Formation and English River Sandstone permits resolution of several correlation problems in the basal Mississippian type sequence. On the basis of its diverse, distinctive brachiopod fauna, the Glen Park Formation is reinterpreted to include similar thin carbonate beds in Illinois which had been variously termed Glen Park, Hamburg oolite or Horton Creek Formation. If the Illinois Hamburg or Horton Creek beds are placed in the basal Carboniferous *Siphonodella sulcata* Zone, as proposed by Sandberg et al. (1972), then the brachiopod fauna of these same beds demonstrates that the type Glen Park of east-central and southeastern Missouri is of the same age. Because of lithologic similarity and for reasons of priority the name Glen Park is retained for these outcrops in both states. Furthermore, the Glen Park Formation, as used here, is correlated with the calcareous English River Sandstone of southeastern Iowa, which is interpreted as a shoreward shallow water shelf facies of the Glen Park. This thin carbonate facies represents the earliest, but very brief, Carboniferous marine transgression into western Illinois, east-central Missouri and southeastern Iowa.

INTRODUCTION

The Glen Park Formation is a thin, in places oolitic, limestone that is discontinuously exposed in and near the bluffs of the Mississippi River in eastern Missouri and west-central Illinois (see Fig. 1). Its subsurface distribution in Illinois is restricted to the west-central portion of the state (Cluff et al., 1981:fig. 42). The subsurface distribution in Missouri has not been published but probably extends beyond the known outcrop limits. The lithology of the Glen Park is highly variable but always includes calcareous components. At various localities it consists of oolitic limestones, limestone conglomerates, biomicrite, silty or sandy limestones or dolomitic limestones, siltstones, shales, or rarely, sandstones. Mehl (1960) and Conkin and Conkin (1973) have also emphasized that it contains poorly sorted rounded quartz sand grains at every outcrop, at least in the basal beds.

Historical Summary of Stratigraphic Terminology

The name Glen Park was first applied to a limestone member of the Sulphur Springs Formation by Ulrich (1904:110) in a published letter to the director of the Missouri Geological Survey. Ulrich distinguished three members in his new Sulphur Springs Formation: an upper sandstone at the top which he named the Bushberg, a middle oolitic limestone called the Glen Park, and a lower shale which he left unnamed.

Ulrich encouraged Prof. Stuart Weller (Weller, 1906:435) of the University of Chicago to investigate the macrofauna of the Glen Park. Weller's description of the stratigraphy and macrofauna provided the first detailed account of the Glen Park Formation. In this paper Weller compared the Glen Park macrofauna to that which he had recovered from an oolite at Hamburg, Calhoun County, Illinois. The latter was the only other known locality in the Mississippi Valley region that contained any significant portion of the Glen Park macrofauna. Weller (1914) later called the beds at Hamburg, Illinois, the Hamburg oolite, being unaware that the name Hamburg had been used twice previously for Cambrian limestones and Tertiary clays. Weller and St. Clair (1928) described additional Glen Park outcrops in Ste. Genevieve County, Missouri, south of the type section.

Moore (1928:138), citing macrofaunal evidence, considered the Hamburg oolite of Calhoun County, Illinois, to be coeval with the Glen Park of Jefferson County, Missouri, and dropped the name Hamburg in Illinois. Branson and Mehl (1933) and Branson (1944) considered the Glen Park to occur as limestone lenses within the Grassy Creek Shale, but this interpretation has not been accepted by others for both biostratigraphic and lithostratigraphic reasons. Weller and Sutton (1940) and Weller et al. (1948) retained both names, Glen Park and Hamburg and, in the later paper, stated (1948:151) that the Hamburg was best considered a member of the Hannibal Shale. Stainbrook (1950), Rubey (1952), Collinson et al. (1954), Workman and Gillette (1956), and Collinson and Swann (1958), following Moore (1928, 1935), reapplied the name Glen Park to the beds that had been named the Hamburg oolite by Weller (1914) and used by subsequent workers in western Illinois. Rubey (1952) first suggested that the term "formation" was more appropriate for this stratigraphic unit because of its varied lithology, and dropped the appellation "limestone." Mehl (1960) noted that Ulrich (1904) had not designated type sections for his Sulphur Springs Formation and its members and formally designated a type section for the Glen Park Limestone at an old quarry near Glen Park, Jefferson County, Missouri. Collinson (1961) used "Glen Park" in quotes to differentiate it from the type Glen Park which he believed to be substantially older than the Illinois beds because of seeming differences in the conodont faunas. For the next dozen years, Collinson and his colleagues at the Illinois Geological Survey consistently avoided using the name Hamburg because of the above mentioned priority problem and used the term Glen Park within quotes (Collinson et al., 1962; Collinson et al., 1971; Atherton et al., 1975) because of the apparent discrepancy in conodont faunas.

Conkin and Conkin (1973) proposed the name Horton Creek for Collinson's "Glen Park" and for the beds in Illinois referred to by Weller (1914) as the Hamburg oolite. They designated an outcrop on the south bank of Horton Creek, Pike County, Illinois as the type section for their new stratigraphic name, which was proposed as a member of the Hannibal Formation. Cluff et al. (1981) raised Horton Creek to formational rank.

Geographic Distribution and Stratigraphic Relations

As interpreted in this report the Glen Park Formation crops out in Missouri from Ste. Genevieve County in the south to Ralls County in the north with outcrops in most of the intervening counties. Weller and St. Clair (1928) and Moore (1928) reported the occurrence of Glen Park beds in Ste. Genevieve County to the south of the type section. Williams (1943:22; 1957:302) found oolitic "Hamburg" beds near Rensselaer, Ralls County. Mehl (1960) reported outcrops of the Glen Park at a number of localities in Jefferson, Franklin, St. Louis, St. Charles, Warren, and Ste. Genevieve counties. In Pike County, Missouri, Mehl (1960:29) described an outcrop of oolite which he called "Hamburg" because of its occurrence above the Louisiana Limestone and the presumed difference in age from type Glen Park. Martin and Wells (1966:28) also reported fossiliferous Glen Park in St. Charles County.

In Illinois the name Glen Park, as used in this paper and stated above, has been called Hamburg oolite, Glen Park Limestone or Formation, "Glen Park," or Horton Creek Member of the Hannibal or Horton Creek Formation. The Glen Park in Illinois crops out at many places in the bluffs of the Mississippi River in Pike County, more rarely in Calhoun County, and infrequently in Jersey County. Worthen (1870:9–12) first referred to these beds in the vicinity of Hamburg, Calhoun County. Krey (1924:36) described additional exposures in Calhoun and Pike counties. Stainbrook (1950), Rubey (1952), Collinson et al. (1954), Collinson and Swann (1958), Collinson (1961), Collinson et al. (1979) and Collinson et al. (1981) cited numerous Glen Park outcrops in Pike, Calhoun, and Jersey counties.

Subsurface distribution of the Glen Park or associated Kinderhookian sediments in Illinois has been documented by Ball (1952), Workman and Gillette (1956), and Cluff et al. (1981). The latter authors, referring to the Glen Park as the Horton Creek Formation, indicate on their fig. 42 a substantial subsurface distribution of the Glen Park in Illinois with a maximum thickness of about 60 feet in Montgomery and Bond counties, Illinois.

At the type section in Jefferson County, Missouri, the Glen Park is conformable below the Bushberg Sandstone and rests unconformably on the Saverton Shale (called Grassy Creek Shale by Branson and Mehl, 1933). According to Mehl (1960:77), the Glen Park in Missouri unconformably overlies several Ordovician or Devonian formations, including the Kimmswick, Maquoketa, Chattanooga and, possibly, the Plattin. It is usually conformably overlain by either the Bushberg Sandstone or the Hannibal Shale. Mehl (1960:77) indicated that it may be unconformably overlain by the Massie Creek Sandstone in Warren County, Missouri, but the author has recently collected atrypids and stropheodontids in the Massie Creek at its type section, neither of which occur above the Frasnian.

In Illinois, the Glen Park overlies the Louisiana Limestone with a marked erosional unconformity

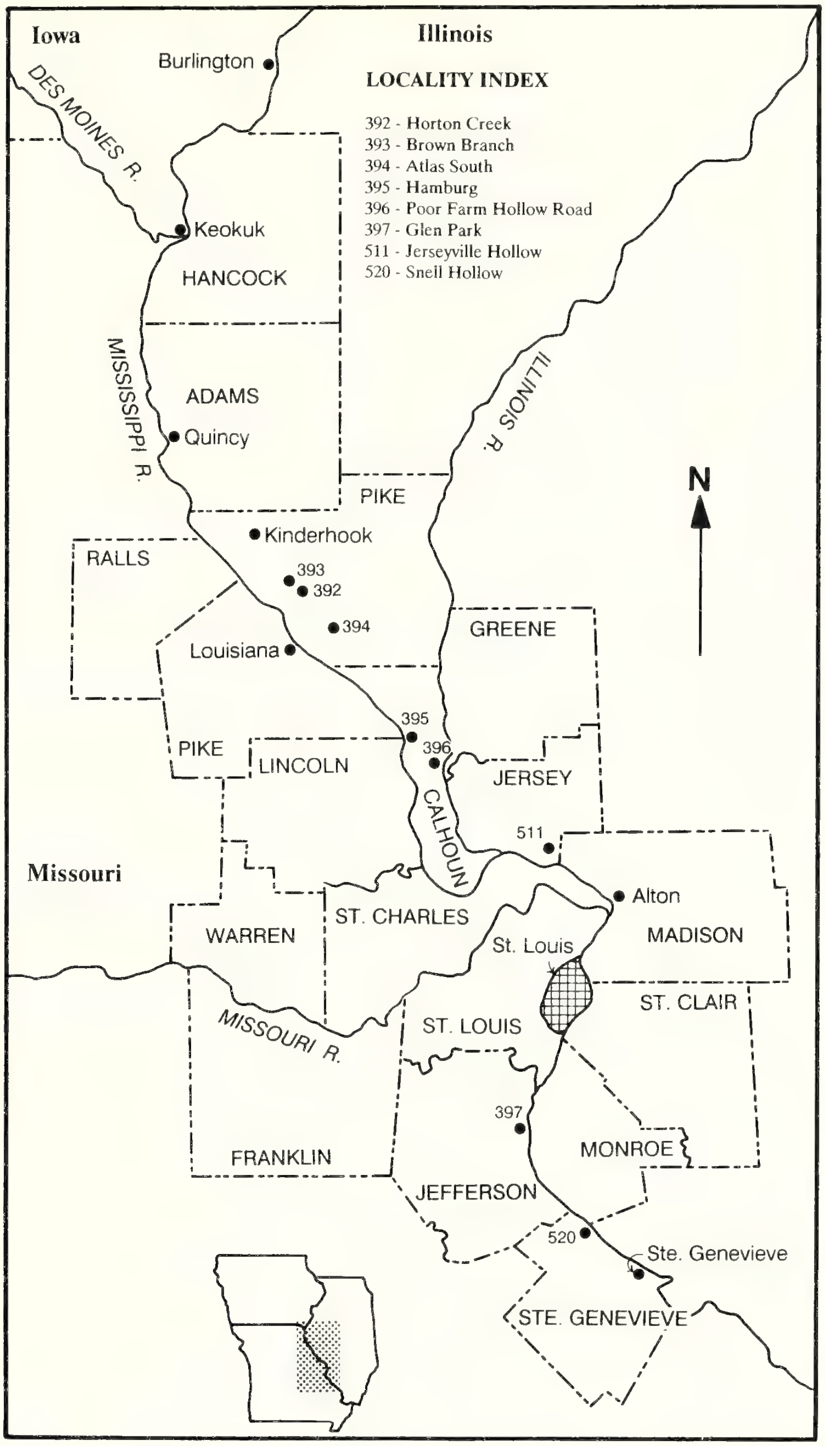


Fig. 1.—Geographic index map showing collecting localities in the Glen Park Formation. The numbers refer to stratigraphic locality collections in The Carnegie Museum of Natural History.

and a basal conglomerate in places, or else with apparent conformity on the Saverton Shale. In the latter cases, Conkin and Conkin (1973) have demonstrated that there is a slight but definite disconformable sedimentary and faunal break at the contact which they have termed a "paracontinuity." In the subsurface, Cluff et al. (1981:47) indicate that the Glen Park may also rest on the Grassy Creek Shale in Madison and St. Clair counties, Illinois.

In western Illinois, the Glen Park is conformably overlain by the Hannibal Shale at all known outcrops. According to Cluff et al. (1981:47), the Glen Park laterally grades into the Hannibal Shale in subsurface eastward but appears to grade laterally into the Louisiana Limestone and Saverton Shale in the subsurface of western Illinois.

AGE AND CORRELATIONS

The precise geologic age of the Glen Park Formation in Missouri has long been in doubt. Although Ulrich (1904) and Weller (1906) suggested that it was probably early Mississippian in age, one must bear in mind that modern notions about the placement of the Devonian-Mississippian boundary differ substantially from those held near the turn of the century.

In recent years, the widespread use of conodont faunal zones, based upon worldwide conodont distributions including those of western Europe, has revolutionized the means for discrimination of this critical boundary. Sandberg et al. (1972) first proposed the modern international conodont zonal scheme for this boundary, defining the latest Devonian as containing the *Siphonodella praesulcata* fauna and the earliest Carboniferous as the base of the *Siphonodella sulcata* Zone. This zonation is now adopted by the IUGS Subcommission on the Devonian-Carboniferous boundary stratotype as the primary means of recognizing the boundary in the northern hemisphere.

In western Illinois, Sandberg et al. (1972:182) noted that Collinson's "Glen Park" and Koenig and Martin's (1961:29, more accurately attributed to M. G. Mehl) "Hamburg oolite" of Pike County, Missouri, in fact contained the *Siphonodella sulcata* Zone fauna and hence were indisputably Carboniferous in age. This conodont zonal scheme used for recognition of the Devonian-Carboniferous boundary is now generally accepted by most biostratigraphers because, at least in the Northern Hemipshere, it is generally consistent and reproducible. In regions where good conodont faunas can be recovered, it provides a biostratigraphic datum from which other faunas and floras that typify this boundary can be correlated.

With this in mind, a brief review of earlier authors' views on the age of the Glen Park, Hamburg, "Glen Park", and Horton Creek is in order. Ulrich (1904), Stuart Weller (1906, 1914), and Moore (1928, 1935), all considered the Glen Park and Hamburg to be early Mississippian in age. Moore (1928, 1935), in fact, dropped the name Hamburg in favor of Glen Park. Weller (1906:466) correlated the Glen Park with the Hamburg of Illinois saying:

> The presence of this fauna at Glen Park and Hamburg may not have been strictly contemporaneous, but its occurrence at the two localities is without doubt associated with the same wave of migration and the fauna at the two localities may be considered to be synchronous within comparatively narrow limits.

Weller and St. Clair (1928:160) reaffirmed this correlation saying:

> In the Hamburg oolite fauna as recorded by Weller, one-half of the species are present also in the Glen Park, and later studies have shown that a still larger portion of the fauna is common to the two formations. The species which do occur in both faunas include two or more peculiar genera which are unknown except in these two faunas. All the evidence at hand points to such a close relationship between the Glen Park and Hamburg faunas that the beds bearing them must be considered as being essentially contemporaneous in origin.

Branson (1938*a*) judged the Glen Park of Missouri to be Devonian in age on the basis of the small macrofauna described by Weller (1906). Later, Branson (1944:174) elaborated saying:

> The Louisiana grades into the Grassy Creek shale in places. Southward the limestone becomes merely lenses in shale. Weller called these lenses the Glen Park and described the fauna as the Glen Park fauna.

In fact, the thicker lenses of Glen Park at its type section often include a basal limestone conglomerate containing large clasts of blue Ordovician Maquoketa Shale, brown micritic Devonian Cedar Valley or equivalent limestone, and greenish gray Saverton Shale of late Famennian age. This obviously indicates a significant erosional unconformity separating the underlying older formations from the sporadically developed limestone lenses of the Glen Park, at least at Glen Park in Jefferson County.

J. M. Weller et al. (1948) correlated the Glen Park of Missouri with the Hamburg beds of Illinois on the basis of faunal similarity and placed them in the Mississippian saying:

> . . . they are clearly part of the Upper Kinderhookian succession, and the Hamburg is best considered a member of the Hannibal.

Note, however, that in this case all of their Lower Kinderhookian is now considered to be of Famennian age.

Mehl (1960:78) found no convincing evidence that confirmed or denied correlation of the type Glen Park with the Hamburg beds of Illinois. Concerning the conodont fauna of the type Glen Park, Mehl said:

> The conodonts that have been found in the Glen Park show trituration.

Most of the triturated conodonts were recognized as Devonian forms and were interpreted as admixtures. He added:

> The best evidence of Devonian age of the Glen Park is that in places it is overlain by the Massie Creek sandstone in which fairly abundant megafauna occurs. This fauna, as indicated elsewhere, argues strongly for the Devonian age of the latter.

Mehl's macrofaunal list for the Massie Creek includes Frasnian, Famennian and Mississippian species of brachiopods. As stated above, the author has recently collected Frasnian or older brachiopods in the type Massie Creek, hence it cannot overlie the Glen Park in normal superposition. In a later paper, Mehl (1961:94) said:

> There is great similarity between the megafossils and the spores found in the Glen Park of east-central Missouri and the Hamburg near its type locality in Illinois. The spores strongly indicate Devonian age of both.

Collinson (1961:102) redefined the Kinderhookian in the type region (Mississippi Valley) to include the base of the "Glen Park" (Hamburg oolite) or Hannibal as the bottom of the series. However, his conodont studies of the type Glen Park (1961:105) suggested to him that the type Glen Park was considerably older than the "Glen Park" beds of Illinois. Collinson et al. (1962) defined a new basal Mississippian conodont assemblage zone, the *Gnathodus* n. sp. B—*G. kockeli* Assemblage Zone, for the "Glen Park" and lowest Hannibal in western Illinois. Collinson et al. (1971) changed the zonal name to the *Protognathodus kuehni—P. kockeli* Zone but retained its meaning and age designation at the base of the Carboniferous. Sandberg et al. (1972: 180, 182) suppressed the latter zonal name in favor of the *Siphonodella sulcata* Zone because of the occurrence of the name giver in the "Glen Park" of Illinois, reaffirming its position at the base of the Carboniferous.

Conkin and Conkin (1973), in assigning a new lithostratigraphic name, the Horton Creek, to the Hamburg oolite of Weller (1914) and the "Glen Park" of Collinson (1961), made no attempt to reconcile their new unit with the type Glen Park of Jefferson County, Missouri. They assigned the entire Horton Creek to the Lower Mississippian (basal Kinderhookian) on the basis of its microfaunas but proposed no formal correlations with other stratigraphic units *per se,* although they did discuss the Devonian-Carboniferous boundary elsewhere in the mid-continent.

Atherton et al. (1975) continued to use "Glen Park" in western Illinois as defined by Collinson (1961), assigning it to the New Albany Group of Devonian and Lower Mississippian age. Cluff et al. (1981:47–50) adopted the term Horton Creek as a formational name. On the basis of physical stratigraphic evidence, they suggested that the Horton Creek might very well be Devonian or straddle the Devonian-Mississippian boundary. Collinson (1985: columns 8 and 9) retained the name Horton Creek for Illinois and placed it at the base of the Mississippian sequence. However, in Missouri, Thompson (1987:column 23) correlated the Glen Park of Perry County, south of St. Louis, with the Conewangoan or late Devonian, although he applied the name Horton Creek of Mississippian age to the *Siphonodella*-bearing outcrops north of St. Louis (1986:17–18).

The previous discussion demonstrates the following: 1) Outcrops of a thin arenaceous carbonate stratigraphic unit, often containing oolitic beds, occur at numerous places on both sides of the Mississippi River, in east-central Missouri and west-central Illinois, in a stratigraphic position just below either the Bushberg Sandstone or Hannibal Shale. The subjacent beds vary from Ordovician to Upper

Devonian units in Missouri but are consistently Saverton Shale or Louisiana Limestone in Illinois outcrops; 2) disconformities or "paracontinuities" commonly occur at the base of this unit on both sides of the river, including the type sections of the Glen Park Limestone, the Hamburg oolite, and the Horton Creek Formation; 3) faunal evidence pointing to a definitive age of these beds for many outcrops, including the type Glen Park, is meager, often based upon negative evidence, triturated conodont specimens, or sparse poorly studied macrofaunas; 4) this stratigraphic unit in Illinois and Pike County, Missouri, has been convincingly dated as basal Carboniferous by Collinson (1961) and Sandberg et al. (1972).

Present Study

The distinctive brachiopod fauna described below is based upon faunally diverse collections from the type sections of the Glen Park, Hamburg oolite, and Horton Creek, as well as other fossiliferous outcrops. Table 1 shows the distribution of the entire brachiopod fauna of the Glen Park Formation at each important collecting locality and includes the comparable English River Sandstone fauna in the right hand column. With the exception of the rare punctate orthid referred to here as *Aulacella* n. sp. and the single productid specimen described here as *Quadratia?* sp., every species found in the type Glen Park of Missouri also occurs in the Illinois beds. The most common species at Glen Park, Missouri, are *Schuchertella hardinensis* n. sp., *Subglobosochonetes jerseyensis* n. sp., *Sedenticellula hamburgensis* (Weller), *Rhynchopora hamburgensis* Weller, *Cardiothyris pristina* n. sp., *Tylothyris missouriensis* (Weller), *Zeugopleura jeffersonensis* (Weller), and *Dielasmella compressa* (Weller). In addition, *Plicochonetes? glenparkensis* (Weller), *Axiodeaneia glenparkensis* n. sp., and *Syringothyris extenuata* (Hall) are diagnostic elements of this fauna. Weller (1906) did not report *Sedenticellula hamburgensis* (Weller), *Rhynchopora hamburgensis* Weller, or *Cardiothyris pristina* n. sp. at Glen Park. However, one may speculate that his *Camarotoechia* sp. undet., and his *Seminula* sp. undet. refer to the latter two taxa.

Weller found a single specimen of a true atrypid at Glen Park, which he named *Atrypa infrequens* in 1914. This specimen has a broken lateral extremity that displays a brown sandy micritic limestone internal matrix and surely came from one of the common Middle Devonian limestone clasts that occur in the Glen Park conglomerate lenses at Glen Park, Missouri.

The key exposure for correlation of the Glen Park Limestone is at Brown Branch, Pike County, Illinois (SL 393). The faunas, both macrofauna and microfauna, were discovered by Charles Collinson of the Illinois Geological Survey. The micritic limestones at this locality are richly fossiliferous (Collinson et al., 1979:34, 35) and the brachiopod fauna is the most diverse of the entire Glen Park or, in fact, for this stratigraphic interval in North America. This remarkable fauna contains 34 species of brachiopods in 32 genera. As can be seen in Table 1, nine of 14 species from the type Glen Park occur here. Eight of nine type Hamburg species and 11 of 15 type Horton Creek species are found at Brown Branch. Most intriguingly, 11 English River Sandstone species occur here, including many of the distinctive species that do not range above the English River, such as *Schizophoria hortonensis* n. sp., *Schuchertella hardinensis* n. sp., *Whidbornella curtirostris* (Winchell), *Mesoplica? mesicostalis* (Weller), *Ovatia nascens* n. sp., *Eudoxina subrotunda* (Weller), and *Syringothyris extenuata* (Hall). In addition, Weller (1914), Moore (1928), and Collinson (1961) list several other species from the basal Hannibal near Kinderhook, Illinois (called English River Sandstone by Moore) that also occur at Brown Branch.

To summarize, the brachiopod faunas of every macrofossiliferous locality in the Glen Park of Missouri and the Hamburg or Horton Creek of Illinois seen by this writer are readily correlated with the diverse fauna at Brown Branch, and the latter is clearly correlated with the English River Sandstone of southeastern Iowa and west-central Illinois. The lack of a *Siphonodella sulcata* conodont fauna at the type Glen Park or other Glen Park localities in Missouri is anomalous. However, well preserved indigenous conodonts are known to be rare in oolitic limestones. The type English River Sandstone in southeastern Iowa also bears this early Mississippian *Siphonodella sulcata* conodont fauna (Collinson, 1961:106). But another anomaly in conodont distribution occurs at Burlington, Iowa, where the same English River Sandstone has not produced Mississippian conodonts (Collinson, 1961:106). The lack of early Mississippian *Siphonodella* faunas at some localities is unfortunate, but the implications of the brachiopod distributions are plain: all macrofossiliferous localities in the Glen Park of Missouri, the Hamburg and Horton Creek of Illinois, the lower Hannibal near Kinderhook, Illinois, and

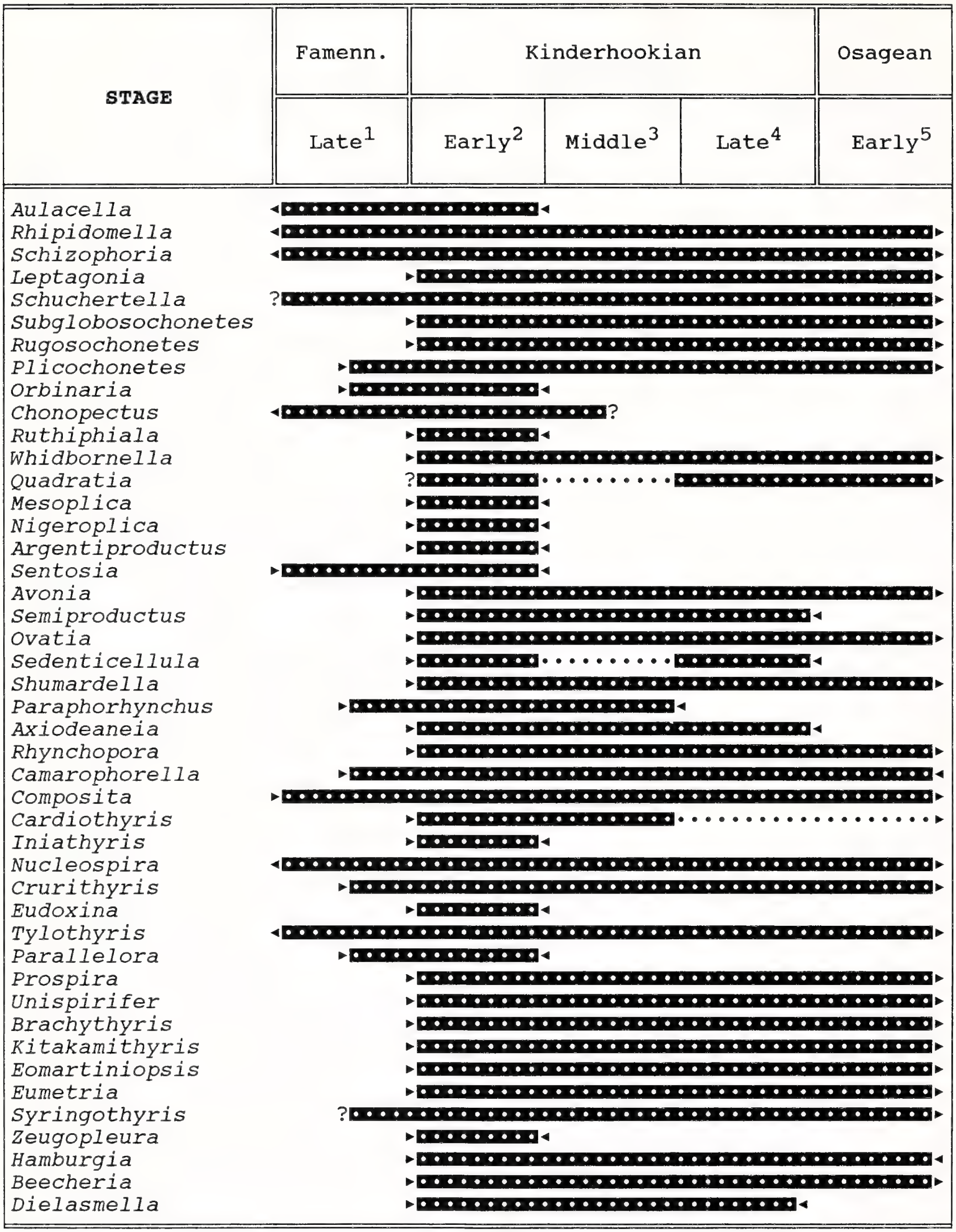
Table 1.—*Distribution of brachiopod species within the Glen Park Formation. Data for the right hand column is for Glen Park species that also occur in the English River Sandstone of southeastern Iowa and west central Illinois.*

	Stratigraphic localities (SL)								
Brachiopod species	392	393	394	395	396	397	511	520	ERS
Lingula sp.			X						X
Orbiculoidea sp.		X							X
Aulacella n. sp.								X	
Rhipidomella rockportensis	X	X	X				X		
Schizophoria hortonensis	X		X						X
Leptagonia cf. *missouriensis*		X							
Schuchertella hardinensis		X		X	X	X	X	X	X
Subglobosochonetes jerseyensis						X	X		
Rugosochonetes pikensis		X							
Rugosochonetes cf. *gregarius*	X	X	X						X
Plicochonetes? glenparkensis	X	X	X	X		X		X	
Orbinaria? brownensis		X							
Ruthiphiala sublaevis		X							X
Whidbornella curtirostris		X							X
Quadratia? sp.						X			
Mesoplica? mesicostalis		X							X
Nigeroplica? illinoisensis	X								
Argentiproductus auriculatus		X							
Sentosia? ignota		X							
Avonia sp.		X							
Semiproductus sp.		X							
Ovatia nascens	X	X							X
Sedenticellula hamburgensis		X		X	X	X		X	
Shumardella fracta	X		X						
Paraphorhynchus sp.		X							X
Axiodeaneia glenparkensis					X	X		X	
Rhynchopora hamburgensis	X	X		X	X	X	X		
Rhynchopora prisca		X							
Camarophorella cf. *buckleyi*		X							
Composita matutina	X	X							
Cardiothryis pristina					X	X			
Nucleospira minima				X	X	X			
Crurithyris cf. *levicula*	X		X						
Tylothyris missouriensis		X	X	X	X	X		X	
Parallelora nupera	X	X	X						
Unispirifer senex		X							
Brachythyris hortonensis	X	X							
Eudoxina subrotunda		X							X
Kitakamithyris cooperensis	X	X	X						X
Eomartiniopsis kinderhookensis	X	X	X						
Syringothyris extenuata	X	X			X	X	X	X	X
Zeugopleura jeffersonensis		X		X	X	X	X	X	
Hamburgia typa		X		X	X			X	
Beecheria paraplicata		X		?	X	X			
Dielasmella compressa		X		X	X	X		X	

the English River Sandstone of southeastern Iowa are the same age and can be confidently correlated. Differences in age due to the rate of transgression from south to north cannot be detected. It is safe to conclude that if this carbonate unit contains the *Siphonodella sulcata* Zone fauna at several outcrops in west-central Illinois and Pike County, Missouri, the entire unit can be considered to be of early Kinderhookian age, including the calcareous English River Sandstone of southeastern Iowa.

Correlations Outside the Mississippi Valley Region

Forty-one genera of articulate brachiopods occur in the Glen Park Formation. Figure 2 shows the stratigraphic distribution of articulate brachiopod


STAGE
Famenn.
Kinderhookian
Osagean
Late1
Early2
Middle3
Late4
Early5
Aulacella
Rhipidomella
Schizophoria
Leptagonia
Schuchertella
Subglobosochonetes
Rugosochonetes
Plicochonetes
Orbinaria
Chonopectus
Ruthiphiala
Whidbornella
Quadratia
Mesoplica
Nigeroplica
Argentiproductus
Sentosia
Avonia
Semiproductus
Ovatia
Sedenticellula
Shumardella
Paraphorhynchus
Axiodeaneia
Rhynchopora
Camarophorella
Composita
Cardiothyris
Iniathyris
Nucleospira
Crurithyris
Eudoxina
Tylothyris
Parallelora
Prospira
Unispirifer
Brachythyris
Kitakamithyris
Eomartiniopsis
Eumetria
Syringothyris
Zeugopleura
Hamburgia
Beecheria
Dielasmella
?
?
?
?

genera in the latest Devonian and early Mississippian of North America. This figure is based upon data from the writer's field collections, museum collections, and all relevant published data that permit confident modern generic assignments. No fewer than 25 genera of articulate brachiopods occur first in the Glen Park Formation. Three other genera occur first in the English River Sandstone, which is considered here to be a near-shore correlative facies of the Glen Park. In addition, 11 genera last occur in the Glen Park and seven are restricted to this interval. The sudden appearance of 28 articulate brachiopod genera at the base of the Kinderhookian, and at or very near the base of the *Siphonodella sulcata* Zone, should facilitate recognition of this important boundary elsewhere.

Although 15 Famennian genera carry over into the Glen Park-English River fauna the appearance of 28 new genera gives the early Kinderhookian faunas a radically different aspect. Several late Famennian brachiopod faunas in North America have been thoroughly described or redescribed by Williams (1943), Cooper and Dutro (1982), and Rodriguez and Gutschick (1967).

The early late Famennian Percha fauna of New Mexico (Cooper and Dutro, 1982:24) contains only four articulate genera that range upward into the Glen Park. Of these four, the genera *Sentosia, Composita,* and possibly *Schuchertella* first appear in the Percha, the punctate orthid genus, *Schizophoria* is long ranging and of less biostratigraphic value. The first occurrence of *Schuchertella* is difficult to ascertain. Cooper and Dutro (1982:54) discuss the problem of distinguishing pseudopunctate and impunctate taxa.

The diverse excellently preserved brachiopod fauna of the very late Famennian Louisiana Limestone bears the late Devonian fauna most similar to that of the Glen Park. Because of its latest Famennian age, as confirmed by the presence of the *Siphonodella praesulcata* conodont fauna, geographic occurrence in the type region of the Mississippian System, and diverse well documented brachiopod fauna, it provides an acceptable datum for discrimination of this horizon for both micro- and macrofaunas.

The brachiopod fauna of the Louisiana Limestone and upper Saverton Shale is well known through the monographic descriptions of Rowley (1908), Weller (1914), and Williams (1943). Large excellent collections are available for study at many institutions as well. Remarkably few Louisiana species appear to carry over into the Glen Park. Only the *Rhipidomella "missouriensis"* and *Camarophorella buckleyi* (Rowley) could be close to or identical with Glen Park species. Comparison at the genus level may be more appropriate. Twelve genera from the Louisiana, mostly long ranging forms, occur in the Glen Park. In North America, six of these first occur in the Louisiana, namely *Plicochonetes, Orbinaria, Paraphorhynchus, Camarophorella, Crurithyris,* and *Parallelora.* Another, *Syringothyris* possibly first occurs here as well. This latter genus is very common in the late Famennian of the eastern United States in beds that cannot be dated by means of conodonts. Until more precise correlations are achieved the range of *Syringothyris* cannot be determined. Two genera, *Orbinaria* and *Parallelora,* occur only in the Louisiana and Glen Park. In general faunal aspect, the Louisiana differs greatly from the Glen Park.

Rodriguez and Gutschick (1967) described several brachiopod faunules from the Sappington Formation of Montana. The faunule from their Unit E was correlated with the Louisiana Limestone. Units F–H appear to be early Kinderhookian (Sando et al. 1969:E9). Some of the brachiopod species described by Rodriguez and Gutschick from their Unit E are closely similar to species in the Glen Park Formation. Their *Schuchertella lens* (White) is more similar to *Schuchertella hardinensis* n. sp. than to the Louisiana Limestone species. Also their *Rhytiophora? arcuatus* (Hall) from Unit E, not Unit F, is comparable to *Nigeroplica? illinoisensis* n. sp. *Beecheria paraplicata* Rodriguez and Gutschick was described from both Units E and F. In the Missis-

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Fig. 2.—North American stratigraphic ranges for articulate brachiopod genera that occur in the Glen Park Formation and the English River Sandstone. [1] Based on occurrences in the Louisiana Limestone and upper Saverton Shale, Percha Shale and Sappington Formation. [2] Based on occurrences in the Glen Park Limestone, English River Sandstone, basal Hannibal Shale of western Illinois and Sappington Formation. [3] Based on occurrences in the Chouteau Limestone and Sedalia Dolomite, upper Hannibal Shale and McCraney through Wassonville sequence. [4] Based on occurrences in the Gilmore City-Eagle City-Maynes Creek facies, Chappel Limestone, upper Northview Shale and "middle" Banff. [5] Based on occurrences in the Meppen, Fern Glen, lower Burlington Limestone, Baird Mountain Member of the St. Joe and "upper" Banff Formation.

sippi Valley it occurs only in the Glen Park Formation. However, some of their species from Unit E, such as *Tylothyris clarksvillensis* (Winchell), do point to a Louisiana Limestone or late Famennian correlation. On the whole, the Unit E faunule appears to be more similar to that of the Glen Park than to that of the Louisiana Limestone.

The small Famennian fauna described from the Pilot Shale of Nevada by Johnson and Reso (1966), and tentatively correlated with the Louisiana Limestone, contains no definitive Glen Park elements. Rodriguez and Gutschick (1967:368) equated their Unit E fauna with that of the Johnson and Reso fauna from the Pilot Shale.

Sando et al. (1969:E9, fig. 4) included a pre-A Zone in their megafaunal zonation scheme for the Carboniferous of the northern Cordillera. Their list of unillustrated taxa from this zone is not incompatible with the Glen Park fauna described below but a direct correlation is not possible under the circumstances.

Thus, the latest Devonian Louisiana Limestone–upper Saverton fauna of the Mississippi Valley is well known, as are some of the late Devonian Cordilleran faunas. The age and correlations of many of these units are well supported by conodont studies. Other smaller Cordilleran brachiopod faunas of probable late Famennian age have been reported by Johnson and Reso (1966) from the Pilot Shale of Nevada, and Rodriguez and Gutschick (1978) from the Leatham Formation of Utah.

Terrigenous clastic beds that span the Devonian-Mississippian boundary occur at many places in the east-central United States. Conodont faunas are generally lacking and placement of the boundary is highly problematical. Few brachiopod faunas have been described. Two such faunas are possibly of basal Mississippian age. Girty (1928) described a small brachiopod fauna from the Riddlesburg Shale Member of the Rockwell Formation in south-central Pennsylvania. One species of this small fauna suggests correlation with the Glen Park Formation. This is *Spirifer compositus* Girty, 1928, which should be referred to the new genus described here as *Zeugopleura*. It appears to be very closely related to *Zeugopleura jeffersonensis* (Weller).

A more diverse fauna has been listed from the Corry Sandstone of northwestern Pennsylvania by Caster (1934) and Sass (1960). Undescribed species in part of the Sass Collection, now deposited at The Carnegie Museum of Natural History, include coarsely denticulate spiriferids of the *Prospira* type and a species of *Ovatia*. These faunal elements may indicate an early, possibly basal, Mississippian age for the Corry, and possible correlation with the Glen Park Limestone. The several species of *Paraphorhynchus* described by Sass (1960) also suggest a Mississippian age, although Williams (1943:83) found a single specimen probably assignable to this genus at the base of the Louisiana Limestone.

Correlations outside North America

Intercontinental correlations for the Carboniferous by means of brachiopods are not common. Most of this reluctance to use brachiopods is due to different interpretations of brachiopod genera and a lack of integrated faunal studies (Brunton, 1984*a*, 1985). Although it is undeniable that some brachiopod faunas are unusually endemic and of limited geographic distribution, in general, the use of brachiopod assemblages shows promise for intercontinental correlation (Brunton, 1984*a*, 1985). In the case at hand, intercontinental correlations made by means of brachiopods are hampered by the lack of information concerning the exact position of the base of the *Siphonodella sulcata* Zone in documented brachiopod bearing beds of Eurasia.

Dehée's (1929) monograph on the fauna of the Etroeungt beds of western Europe provides an invaluable basis for comparisons between North American and western European latest Famennian brachiopod faunas. Unfortunately, no modern work dealing with the early Tournaisian brachiopods of Belgium is available for comparison with North American faunas. Comparison with Devonian-Carboniferous boundary faunas in the Soviet Union is hampered by interpretation of the position of the boundary and the paucity of published conodont occurrences. In a recent paper Fotieva (1985) describes and illustrates many genera of brachiopods from the Famennian-Tournaisian boundary beds of the Timan-Pechora province and the western slope of the Urals. Along with many common Devonian genera she reports the following genera from the Lytvinskiy horizon: *Leptagonia, Spinocarinfera, Nigeroplica, Productina, Ovatia, Unispirifer, Punctospirifer,* and *Dielasma.* Although this horizon is attributed to the early Carboniferous by Fotieva, the more complete faunas listed for the Lytvinskiy horizon by Sultanaev (1975:5–9) include Devonian conodonts, clymenid ammonoids, and numerous Etroeungt-type brachiopods. These faunal elements are interpreted here to indicate a late Famennian age for the Lytvinskiy. None of the genera listed above has been reported in the Famennian of North America. In the superjacent (early Carboniferous) horizon Fotieva reports the presence of *Eomartiniopsis, Eudoxina, Cleiothyridina,* and *Cardiothyris* which also occur first in the Glen Park Formation in North America. Thus, it appears that many brachiopod genera that first occur in the Glen Park in North America first occur in Famennian age rocks in the Soviet Union, as interpreted by this writer.

FOSSILIFEROUS SEDIMENTARY FACIES

In general, the Glen Park Formation is sparsely fossiliferous and most Glen Park outcrops lack macrofossils. Brachiopods are the most common macrofossils but molluscs are abundant at the type section of the formation. Other macro-invertebrates are very rare. The brachiopods occur in only several of the many Glen Park lithologies, namely, biomicrite, oosparite, silty dolomite or dolomitic limestone, and calcareous sandstone or arenaceous limestone. Invariably, they are found in only one lithology at each collecting locality, often only in one bed.

Many benthonic marine invertebrates are often referred to as "facies fossils" and are presumed to have very limited distribution in various sedimentary environments. In fact, as pointed out by Brunton (1984*a*:38), fossil articulate brachiopods are found in most normal marine sedimentary rock types except those that indicate extremely rapid sedimentation or contain excessive amounts of clay-sized particulates held in suspension. Table 2 shows the occurrences of Glen Park brachiopods in the four fossiliferous types of carbonate or carbonate cemented sediments of the Glen Park. By far the most diverse fauna occurs in the thin biomicrite at Brown Branch (SL393). Of the 34 species that occur here, ten are known only from this facies. Another 11 species also occur in two or three other facies, indicating probable eurytopic adaptation to bottom conditions for these species, assuming these species were indigenous to their collecting localities. The other 16 species occur in two of the fossiliferous facies. The distribution of species in the other remaining three facies is even more dispersed. All ten species from the spar-cemented oolite at Hamburg (SL395) occur in one or more other facies, and this entire faunule may be allochthonous. Only three of 17 species from the silty dolomitic facies (SL392 and SL394) are unique to this lithology and only four of 26 species that occur in calcareous sandstone or arenaceous limestones are limited to that depositional environment.

Twenty-seven of the 45 species described in this report occur in more than one sedimentary facies and several of the 17 restricted species are so rare as to be represented by only a few individuals or even a single specimen. Very similar younger articulate brachiopod faunal distributions occur in the Prospect Hill Sandstone, Starr's Cave Oolite and Wassonville Dolomite of southeastern Iowa and micritic Chouteau Limestone and Sedalia Dolomite of Missouri. It may be concluded that, at least in Lower Mississippian normal marine shelf sediments, many articulate brachiopod species could tolerate a variety of substrates and sediments.

Williams (1957) interpreted the oolitic beds of the Glen Park to represent deposition in very shallow water which may have been withdrawn from time to time. This was suggested by cross-bedding, ripple marks, and the lenticular nature of the oolitic beds. Distribution of the "Horton Creek" facies which includes these oolites in Illinois is well shown by Cluff et al. (1981:fig. 42) but, unfortunately, they were not able to differentiate and map its temporal equivalents, the English River Sandstone (or lower Hannibal Shale) from other New Albany Group sediments. Their interpretation of the distribution of the basin and shelf facies and general paleogeography for the entire New Albany Group (Cluff et al. 1981:59, 60, fig. 48) probably applies equally well to the restricted early Kinderhookian interval of the Glen Park and English River or lower Hannibal.

The erosional surfaces sometimes recorded at places in the basal beds of the Glen Park, occasional conglomerate beds, and thin basal quartz sandstones or thin layers of rounded sand grains at the base of the Glen Park, suggest a short but definite erosional hiatus at the end of the Devonian, reflecting a brief withdrawal or shallowing in at least part of the northern or Mississippi Valley marine lobe of the late Devonian mid-continental seaway. The oosparites, biomicrites, silty dolomites and arenaceous limestones or calcareous sandstones of the Glen Park are facies that record a brief, rapid, very shallow marine transgression that extended northward from

Table 2.—*Occurrences of brachiopods according to sedimentary facies. The right hand column includes Glen Park species that also occur in the calcareous sandstone of the English River Formation at Kinderhook, Illinois, and near Burlington, Iowa.*

	Sedimentary facies			
Brachiopod species	Bio-micrite	Oo-sparite	Silty Dol.	Aren. Ls. or Calc. Ss.
Lingula sp.			X	X
Orbiculoidea sp.	X			X
Aulacella n. sp.				X
Rhipidomella rockportensis	X		X	X
Schizophoria hortonensis			X	X
Leptagonia cf. *missouriensis*	X			
Schuchertella hardinensis	X	X		X
Subglobosochonetes jerseyensis				X
Rugosochonetes pikensis	X			
Rugosochonetes cf. *gregarius*	X		X	X
Plicochonetes? glenparkensis	X	X	X	X
Orbinaria? brownensis	X			
Ruthiphiala sublaevis	X			X
Whidbornella curtirostris	X			X
Quadratia? sp.				X
Mesoplica? mesicostalis	X			X
Nigeroplica? illinoisensis			X	
Argentiproductus auriculatus	X			
Sentosia? ignota	X			
Avonia sp.	X			
Semiproductus sp.	X			
Ovatia nascens	X		X	X
Sedenticellula hamburgensis	X	X		X
Shumardella fracta			X	
Paraphorhynchus sp.	X			X
Axiodeaneia glenparkensis				X
Rhynchopora hamburgensis	X	X	X	X
Rhynchopore prisca	X			
Camarophorella cf. *buckleyi*	X			
Composita matutina	X		X	
Cardiothyris pristina				X
Nucleospira minima		X		X
Crurithyris cf. *levicula*			X	
Tylothyris missouriensis	X	X	X	X
Parallelora nupera	X		X	
Unispirifer senex	X			
Brachythyris hortonensis	X		X	
Eudoxina subrotunda	X			X
Kitakamithyris cooperensis	X		X	X
Eomartiniopsis kinderhookensis	X		X	
Syringothyris extenuata	X		X	X
Zeugopleura jeffersonensis	X	X		X
Hamburgia typa	X	X		X
Beecheria paraplicata	X	?		X
Dielasmella compressa	X	X		X

southern Missouri and Illinois into central Iowa, approaching the Transcontinental Arch, at the beginning of the Carboniferous, rapidly reoccupying much of the same region in which the Saverton-Louisiana-Maple Mill had been deposited in the very late Famennian.

Preservation

Preservation of adult shells is the norm at most collecting localities, but the high-energy sedimentary environments indicated by the varied Glen Park lithofacies precluded the retention of much micro-ornament. Most shells show some evidence of abrasion. Except for the *Rhipidomella rockportensis* n. sp., *Schizophoria hortonensis* n. sp., *Parallelora nupera* n. sp., *Eomartiniopsis kinderhookensis* n. sp., and *Kitakamithyris cooperensis* (Swallow) from locality SL392, complete specimens of strophic species could not be found at other localities, including the very diverse fauna from the biomicrite at locality SL393. Complete specimens of rostrate species, however, are common for the following species: *Sedenticellula hamburgensis* (Weller), *Rhynchopora hamburgensis* Weller, *Dielasmella compressa* (Weller), and *Shumardella fracta* n. sp. Several rare complete shells of *Hamburgia typa* Weller, *Crurithyris* cf. *levicula* (Rowley) and *Nucleospira minima* Weller were also found.

Cloud (1948) commented on the small size of the brachiopods found in the "Hamburg oolite" in his discussion of assemblages of diminutive brachiopods. He concluded that the concentration of small specimens in his Glen Park collections were the result of current action. His prediction that larger adult stages of the tiny Hamburg juveniles would be found in laterally equivalent rocks is only partially borne out by this study. The most common species recovered by this writer from the oosparite at Hamburg, Illinois, include small *Schuchertella hardinensis* n. sp., small *Sedenticellula hamburgensis* (Weller), normal adult-sized *Rhynchopora hamburgensis* Weller, medium to large *Tylothyris missouriensis* (Weller), large *Dielasmella compressa* (Weller), large *Nucleospira minima* Weller, and medium to large *Hamburgia typa* Weller. The *Schuchertella hardinensis* n. sp. and *Sedenticellula hamburgensis* (Weller) do reach their largest adult size elsewhere, the former in the arenaceous limestone at locality SL396, and the latter at localities SL393 and SL397 (type Glen Park).

Punctation in *Rhynchopora hamburgensis* Weller and *Zeugopleura jeffersonensis* (Weller) is ordinarily difficult to detect at most collecting localities. Also, the characteristic syringothyridid micro-ornament of the latter species was preserved in only a few of the hundreds of specimens used in this study.

FAUNAL COMPOSITION

The fauna described below contains representatives of almost every major brachiopod group that is normally found in Kinderhookian strata of North America. Figure 2 and Tables 1 and 2 give the generic composition of the fauna and species distribution. There are two inarticulates, three punctate orthids, two strophomenids, four chonetids, eleven productids, one pentamerid (stenoscismatacean), three impunctate rhynchonellids, two punctate rhynchonellids, four athyridids, eight impunctate spiriferids, two punctate spiriferids (syringothyridids), and three terebratulids. No major brachiopod group found in younger Kinderhookian beds is missing although some groups are poorly represented when compared with their abundance in late Famennian strata.

Inarticulates.—Only two genera are represented here and specimens are very rare. The long-ranging genera *Lingula* and *Orbiculoidea* are of little biostratigraphic value.

Punctate orthids.—The genera *Aulacella, Rhipidomella* and *Schizophoria* are all long ranging. The specimens identified here as *Aulacella* n. sp. represent the first report of this genus in well-dated Mississippian rocks in North America. *Rhipidomella rockportensis* n. sp. is similar to the Chouteau species widely identified as *Rhipidomella missouriensis* (Swallow), an invalid name, and may have an extensive stratigraphic range. *Schizophoria hortonensis* n. sp. appears to be a distinctive short-ranging species.

Strophomenids.—Leptagonia, not present in the late Famennian, first appears at a single locality in the Glen Park Formation. The species identified here as *Leptagonia* cf. *L. missouriensis* Carter may range throughout the Kinderhookian into the early Osagean. The only Glen Park orthotedid, *Schuchertella hardinensis* n. sp., seems to be restricted to this horizon.

Chonetids.—Plicochonetes? glenparkensis (Weller) may be related to *Plicochonetes ornatus* (Shumard) but certainly not closely. The former has rounded ears and is not similar to the Chouteau species commonly identified as *Chonetes glenparkensis* Weller. The Bushberg species cited by Branson (1938*a*) is not conspecific with the Glen Park species and the latter may be restricted to the Glen Park and its correlatives. To the writer's knowledge all non-Glen Park identifications of *Plicochonetes*? *glenparkensis* in the literature are incorrect. *Rugosochonetes gregarius* (Weller) was described from a thin oolitic limestone that occurs just above the English River Sandstone at Burlington, Iowa. That thin limestone is probably a Glen Park equivalent as is the upper fossiliferous part of the English River. The other two chonetids, *Rugosochonetes pikensis* n. sp. and *Subglobosochonetes jerseyensis* n. sp., may be restricted to the Glen Park.

Productids.—The productid portion of the brachiopod fauna is diverse and includes 11 species in 11 different genera. Compare this with 16 species in 12 genera of the Chouteau or only seven species in seven genera in the entire McCraney through Wassonville sequence of southeastern Iowa. Four genera are productellids, two of which, *Orbinaria* and *Whidbornella,* indicate strong Devonian affinities. Three genera are leioproductids. Again, two of these, *Mesoplica* and *Nigeroplica,* first appear in the late Famennian in Europe and the Soviet Union. Three avoniid genera are present, one of which, *Sentosia,* is previously known mainly from the Percha Shale of late Famennian age. The linoproductid genus *Ovatia* represents a Carboniferous and Permian lineage. The other genera not discussed here are of Carboniferous aspect. Nine of the 11 productid genera first occur at this horizon in North America.

Pentamerids.—Following Rudwick (1970) I consider the stenoscismataceans to be derived from the pentamerids. One such genus, *Sedenticellula,* occurs here. This rare genus is known only from the Glen Park and Chappel limestones of Kinderhookian age.

Rhynchonellids.—Four genera of rhynchonellids, all of Carboniferous aspect, occur in the Glen Park. The first appearances of *Axiodeaneia* and *Shumardella* are considered significant. Two species of the common Permo-Carboniferous genus *Rhynchopora* in the Glen Park mark the first appearance of this genus at the base of the Carboniferous.

Athyridids.—Four genera are present, three of which have Devonian representatives. Only the *Cardiothyris* is restricted to the Mississippian.

Impunctate spiriferids.—There are eight species in as many genera. The genera *Crurithyris, Tylothyris* and *Parallelora* have late Famennian predecessors but the other five genera have their first occurrence in the Glen Park. The ambocoeliid genus *Eudoxina* and two reticulariacean genera, *Eomartinioposis* and *Kitakamithyris,* first occur here in North America.

Punctate spiriferids.—Two syringothyridid genera are the only punctate spiriferids in the Glen Park. The genus *Syringothyris* is common in Famennian strata in several continents and is of limited biostratigraphic utility. On the other hand, the new genus *Zeugopleura* may prove to be restricted to the early Kinderhookian Glen Park interval.

Terebratulids.—Three species in three genera of terebratulids occur in the Glen Park. Probably all three mark their first occurrence at the base of the Kinderhookian. Although none of these genera occurs together in younger Kinderhookian formations of the mid-continent all three genera occur together in the Chappel Limestone of central Texas in beds judged to be of very late Kinderhookian age.

PREVIOUS MEGAFOSSIL STUDIES

Weller (1906) first described a portion of the macrofauna of the Glen Park Formation in his paper dealing with the type Glen Park at Glen Park, Jefferson County, Missouri. In 1914, Weller described several additional Glen Park species from the Hamburg oolite of Calhoun County, Illinois. Branson (1938*a*) repeated Weller's descriptions and reillustrated Weller's types but added no new information concerning the biological or geographic extent of the brachiopod fauna. No new Glen Park brachiopod taxa have been described since Weller's studies.

ACKNOWLEDGMENTS

The discovery by Charles Collinson of the unusually diverse brachiopod fauna at Brown Branch, Pike County, Illinois, provided the stimulus for preparation of this report. His generous loan of the rock samples and encouragement to prepare and describe the fauna are much appreciated. Albert Kollar of The Carnegie Museum of Natural History prepared many excellent transverse serial sections. The author is also indebted to the following individuals who lent type specimens: Daniel Blake of the University of Illinois, Daniel Fisher of the University of Michigan, Matthew Nitecki of the Field Museum of Natural History, and James Stitt of the University of Missouri.

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ACRONYMS

The following acronyms are used in this report: CM, The Carnegie Museum of Natural History; FMNH, the Field Museum of Natural History; UMI, University of Michigan Museum of Paleontology; UI, the University of Illinois; IGS, the Illinois State Geological Survey; UMO, the University of Missouri; and UND, the University of Notre Dame.

STRATIGRAPHIC LOCALITIES (SL)

SL392—*Horton Creek,* Illinois. Glen Park Formation in bluff overhanging south bank of creek. NW ¼, NW ¼, sec. 6, T. 6 S., R. 5 W., Rockport Quad., Pike Co., IL. CM Collection.

SL393—*Brown Branch,* Illinois. Glen Park Formation in bluff above south bank of creek. Basal micritic limestone bed with geodes and conglomeratic clasts at east end of bluff highly fossiliferous. SW ¼, N ½, sec. 26, T. 5 S., R. 6 W., Rockport Quad., Pike Co., IL. IGS and CM collections.

SL394—*Atlas South,* Illinois. Glen Park Formation in hillside above Illinois 96, 2.1 miles southeast of Atlas, IL. Center SE ¼, sec. 35, T. 6 S., R. 5 W., Pleasant Hill West Quad., Pike Co. IL. IGS and CM collections.

SL395—*Hamburg,* Illinois. Oolite bed near top of Glen Park Formation exposed in creekbed and bank of Irish Hollow Creek, behind Methodist Church. NW ¼, SE ¼, sec. 35, T. 9 S., R. 3 W., Hamburg Quad., Calhoun Co., IL. CM collection.

SL396—*Poor Farm Hollow Road,* Illinois. Glen Park Formation in creek bank on south side of Poor Farm Hollow Road, about

1.1 miles west of Illinois 100. SW ¼, NW ¼, sec. 22, T. 10 S., R. 2 W., Hamburg Quad., Calhoun Co., IL. IGS and CM collections.

SL397—*Glen Park,* Missouri. Glen Park Formation from an abandoned quarry (formerly the Goetz Quarry). Center N ½, sec. 5, T. 41 N., R. 6 E., Herculaneum Quad., Jefferson Co., MO. FMNH types and CM collection.

SL511—*Jerseyville Hollow,* Illinois. Glen Park Formation (called Hamburg by collector). SE ¼, sec. 3, T. 6 N., R. 12 W., Grafton Quad., Jersey Co., IL. IGS collection, collected by Tracey Gillette, 1942.

SL520—*Snell Hollow,* Missouri. Glen Park Formation exposed above NW bank of creek. NW ¼, SW ¼, SE ¼, sec. 24, T. 39 N., R. 7 E., Bloomsdale Quad., Ste. Genevieve Co., MO. CM collection.

DEPOSITION OF SPECIMENS

Except for the type specimens borrowed from other museum and university collections, all of the types and referred specimens of this report are deposited at the Illinois State Geological Survey in Champaign, Illinois, or The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

SYSTEMATIC PALEONTOLOGY

The suprageneric classification given herein mainly follows that of the Treatise on Invertebrate Paleontology or that of Cooper and Grant (1972–1977). Open nomenclature and synonomies are arranged and marked following the method of Richter (1948), as described by Matthews (1973).

Phylum Brachiopoda Duméril
Class Inarticulata Huxley
Order Lingulida Waagen
Superfamily Lingulacea Menke
Family Lingulidae Menke
Genus ***Lingula*** Bruguière, 1797

Lingula sp.
Fig. 3.1

Remarks.—A single specimen of this genus has been found in the Glen Park. It is a very small single valve, about 7.1 mm long, orientation unknown, from locality SL394.

Order Acrotretida Kuhn
Suborder Acrotretidina Kuhn
Superfamily Acrotretacea Schuchert
Family Discinidae Gray
Subfamily Orbiculoideinae Schuchert
Genus ***Orbiculoidea*** D'Orbigny, 1847

Orbiculoidea sp.
Fig. 3.2–3.4

Remarks.—Five small, rounded inarticulate brachial valves from locality SL393 are assignable to the common genus *Orbiculoidea.* The largest of these shells is nearly circular and about 5.3 mm in maximum dimension. These brachial valves are similar in size and shape to the form described by Moore (1928:262) as *Orbiculoidea hardinensis,* which he recovered from the base of the Hannibal Shale in Calhoun County, Illinois. However, the diagnostic characters of this species are found in the pedicle valve.

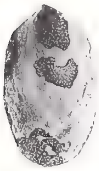
Class Articulata Huxley
Order Enteletida Waagen
Superfamily Rhipidomellacea Alichova
Family Oniellidae Öpik
Genus ***Aulacella*** Schuchert and Cooper, 1931

Aulacella n. sp.
Fig. 5.13–5.15

Remarks.—Five disarticulated incomplete specimens of this Late Devonian genus were recovered from locality SL520 in a southern sandstone facies of the Glen Park Formation, Ste. Genevieve Co., Missouri. Although this species is undoubtedly undescribed, the poor preservation of the few available specimens and lack of interiors prevents proposal of a new taxon.

Assignment to the genus *Aulacella* is based on external characters, including the strong ventral fold, distinct dorsal sulcus, and fascicostellate ornament. It is possible that Weller and St. Clair (1928:161) referred to this species as *Rhipidomella* sp. undesc. in their faunal list from the same locality.

This species is a tiny one; the largest specimen is about 5.2 mm long with a width of about 6.4 mm.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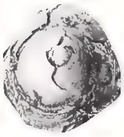
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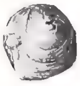
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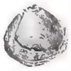
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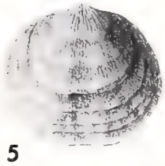
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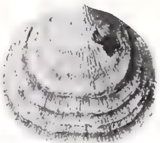
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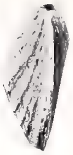
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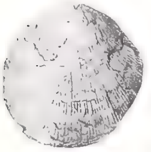
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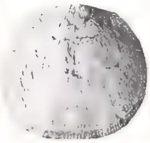
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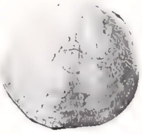
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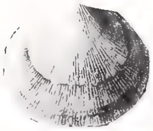
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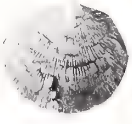
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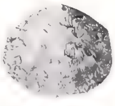
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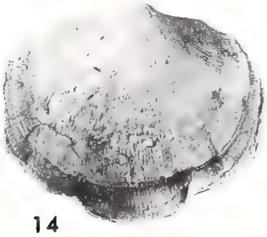
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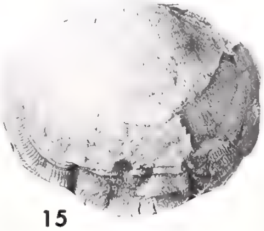
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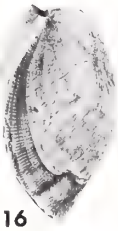
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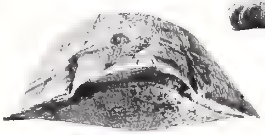
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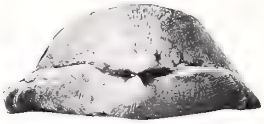
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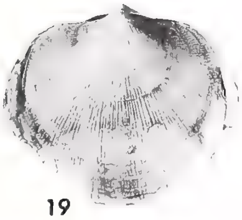
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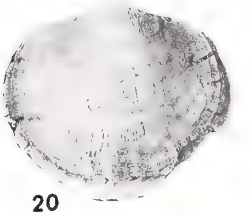
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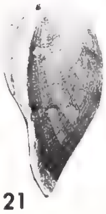
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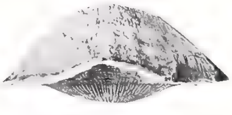
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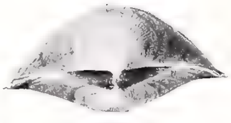
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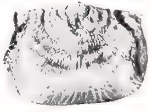
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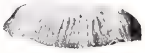
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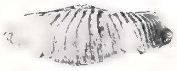
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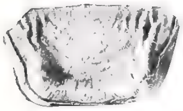
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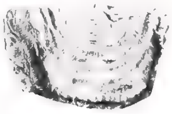
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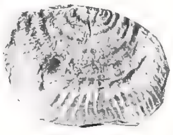
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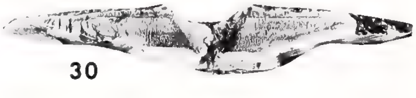
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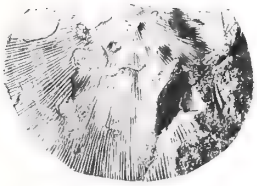
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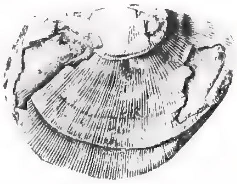
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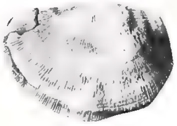
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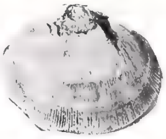
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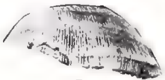
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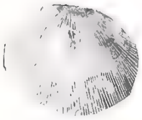
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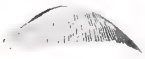
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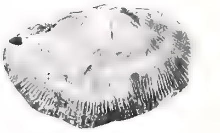
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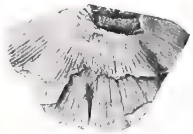
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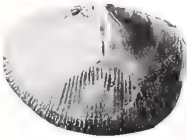
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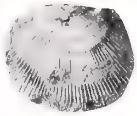
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The pedicle valve is strongly arched with nearly flat flanks and the brachial valve is almost planar except for the medial sulcus.

This species is not similar to the several Devonian forms from Iowa and New Mexico described or illustrated by Cooper and Dutro (1982), being much smaller and having a planar brachial valve and more distinctly fasciculate ornament. Nor is it close to the Soviet taxa recently described by Beznosova (1963), Grechishnikova (1966), Bublichenko (1971) and Nalivkin (1979), most of whom refer their taxa to *Aulacella interlineata* (Sowerby), an Upper Devonian species. This Glen Park species is possibly most similar in outline and size to the Pilton shells illustrated by Whidborne (1897:165, pl. 20, fig. 8, 9) as *Orthis* sp., although the finer ribbing in the latter is very poorly indicated in the illustrations and its systematic position is not clear to this writer.

Family Rhipidomellidae Schuchert
Genus ***Rhipidomella*** Oehlert, 1890

Rhipidomella rockportensis, new species
Figs. 3.5–3.13

Holotype.—CM 34618, Fig. 3.5–3.7, collected by the author from locality SL392, April, 1983.

Paratypes.—CM 34619–34623, same collection as the holotype. IGS 80P5 from SL511.

Description.—Medium size for genus, unequally biconvex with brachial valve more inflated than pedicle valve; outline subcircular to transversely subovate with maximum width attained at or slightly anterior to midlength; lateral profile semi-guttate; hingeline narrow, lateral extremities well rounded in all growth stages; anterior commissure nearly rectimarginate to very weakly sulcate, slightly emarginate; fold and sulcus lacking; ornament consisting of numerous fine costellae and strong, irregularly spaced growth varices.

Pedicle valve weakly convex or almost flat in lateral profile, except in umbonal region; beak small, acute, slightly incurved; interarea very small, apsacline, slightly concave; delthyrium broad, nearly forming equilateral triangle with teeth; beak ridges angular, well defined; anterior profile weakly and evenly convex or most convex medially with flattened flanks; no sulcus produced in any specimen at hand; interior not observed.

Brachial valve much more convex than opposite valve, evenly convex to slightly flattened medially, most convex umbonally and anteriorly; anterior profile variable from evenly convex to slightly flattened or with weak sulcus; beak tiny, inconspicuous; interarea much reduced, probably orthocline; fold absent but shallow sulcus in some specimens producing slightly emarginate outline; interior not observed.

Distinguishing characters.—This species is characterized by its flattened or slightly sulcate dorsum, weakly emarginate outline, and evenly convex venter, lacking a ventral sulcus.

Remarks.—*Rhipidomella missouriensis* (Swallow), originally *Orthis missouriensis* Swallow, 1860, was most likely named from the Kinderhookian Chouteau Limestone (Branson, 1938*a*:42). It has commonly been identified in the late Famennian Louisiana Limestone of Missouri and Illinois, and is a junior objective synonym of *Orthis missouriensis* Shumard, 1855, a Silurian impunctate orthid. This Glen Park species is closely similar to the unnamed Chouteau and Louisiana Limestone species and could be conspecific. The Louisiana Limestone specimens examined by the author tend to be more subquadrate and the pedicle valves are slightly flatter medially but these small differences could well be taxonomically unimportant.

The other Chouteau species of *Rhipidomella, R. tenuicostata* Weller, 1914, is not similar to *Rhipidomella rockportensis* n. sp., being more nasute with finer costellae.

Distribution.—This species occurs at the following Glen Park localities: SL392 (42 specimens), SL393 (19 specimens), SL394 (8 specimens), IGS-Gillette Coll. 790, SL 511, Jerseyville Hollow, Jersey County, Illinois (1 specimen). All of these occurrences except the last one are from the non-oolitic silty dolomitic facies.

←

Fig. 3.—Inarticulates, punctate orthids, and strophomenids. 3.1, *Lingula* sp., valve unknown, from SL394, ×3, IGS 80P1. 3.2–3.4, *Orbiculoidea* sp., three branchial valves from SL393, ×3, IGS 80P2–80P4. 3.5–3.13, *Rhipidomella rockportensis* n. sp.; 3.5–3.7, ventral, dorsal and lateral views of the holotype from SL392, CM 34618; 3.8–3.10, 3.12, 3.13, three brachial valves and two pedicle valves, respectively, CM 34619–34623 from SL392; 3.11, a pedicle valve from SL511, IGS 80P5, all ×1 except 3.5–3.7, ×1.5. 3.14–3.23, *Schizophoria hortonensis* n. sp., ventral, dorsal, lateral, anterior and posterior views of the holotype (3.14–3.18) and a paratype from SL392, CM 34624, 34625, ×1. 3.24–3.29, *Leptagonia* cf. *L. missouriensis* Carter; 3.24, pedicle valve, IGS 80P6; 3.25, a brachial valve, IGS 80P7; 3.26–3.29, ventral and anterior views of two pedicle valves, CM 34626, 34627, all from SL393, all ×1. 3.31–3.41, *Schuchertella hardinensis* n. sp.; 3.30, 3.32, posterior and ventral views of a pedicle valve from SL396, the holotype, CM 34628, ×2 and ×1, respectively; 3.31, a large pedicle valve from SL396, CM 34629, ×1; 3.33, a brachial valve from SL396, CM 34630, ×1; 3.34–3.37, dorsal and anterior views of two small brachial valves from SL396, CM 34631, 34632, ×1; 3.38, 3.39, a brachial valve and a pedicle valve from SL393, IGS 80P8, 80P9, ×1; 3.40, 3.41, two small brachial valves from SL393, CM 34633, 34634, ×1.5.

Table 3.—*Measurements of types (in mm) of* Rhipidomella rockportensis, *new species.*

Specimen no.	Locality	Length	Width	Thickness
Holotype				
CM 34618	SL392	13.1	14.5	5.7
Pedicle valves				
IGS 80P5	SL511	17.2	19.4	4.0
CM 34622	SL392	15.9	17.3	4.2
CM 35623	SL392	13.0	15.2	2.2
Brachial valves				
CM 34619	SL392	19.6	20.2	6.9
CM 34620	SL392	19.8	19.9	6.3
CM 34621	SL392	17.8	18.6	6.3

Family Enteletidae Waagen
Subfamily Schizophoriinae Schuchert
Genus ***Schizophoria*** King, 1850

Schizophoria hortonensis, new species
Figs. 3.14–3.23

Holotype.—CM 34624, Fig. 3.14–3.18, collected by the author from locality SL392, May 1983.

Paratype.—CM 34625, same collection as the holotype.

Description.—Medium size for genus, dorsibiconvex, transversely subelliptical in outline, greatest width near midlength; lateral profile guttate; hingeline about half of maximum width; cardinal extremities well rounded.

Pedicle valve moderately convex, much thinner than brachial valve, compressed at cardinal extremities, most convex in umbonal region; surface sloping evenly to lateral and anterior margins, becoming almost resupinate in lateral profile in some specimens; umbonal region moderately inflated and moderately broad; shallow, broad sulcus developed in anterior half of valve; beak small and slightly incurved; ventral interarea low, acutely triangular, marked by weak transverse ridges, well defined by subangular beak ridges, moderately concave, apsacline to almost catacline; delthyrium of moderate size, slightly narrower than high; internal details not observed.

Brachial valve much more inflated and convex than pedicle valve, being most convex in umbonal region, surface sloping steeply toward cardinal margin, more evenly towards lateral and anterior margins, becoming slightly compressed towards cardinal margins; umbonal region inflated and projecting well posterior to hingeline; median fold not differentiated; beak tiny, slightly incurved; dorsal interarea concave, very low, apsacline; interior not observed.

Distinguishing characters.—This species can be differentiated by its transversely subelliptical outline, thin pedicle valve, and strongly convex brachial valve, lacking a discernable fold.

Table 4.—*Measurements of the types (in mm) of* Schizophoria hortonensis *n. sp. from locality SL392.*

Specimen no.	Length	Width	Thickness
CM 34624	30.4	35.3	18.4
CM 34625	27.1	31.5	14.9

Remarks.—The description above is based mainly on the two figured complete but slightly crushed specimens from locality SL392, Pike County, Illinois. The species is moderately common in the silty dolomitic facies along the bluffs of the Mississippi River from Horton Creek to well south of Atlas in Pike County. It is not known to occur in the oolitic facies of the Glen Park. The specimens from the English River Sandstone illustrated by Weller (1914: pl. 21, figs. 33, 34) may belong here but more and better preserved English River specimens are needed to confirm this possible identification.

Schizophoria williamsi Rodriguez and Gutschick, 1978, from the Late Famennian Leatham Formation of Utah is similar in size and outline to *Schizophoria hortonensis* n. sp., but differs in having a more inflated pedicle valve, a less inflated brachial valve, and in being somewhat more transverse.

Schizophoria hortonensis n. sp. is most similar to *Schizophoria poststriatula* Weller, 1914, from the Fern Glen Formation of Missouri and the Banff Formation of Alberta. The latter can be distinguished by its more subquadrate outline and better developed sulcus. Weller (1914:167) stated that *poststriatula* lacked a median flattening or sulcus on the brachial valve. However, one of Weller's types (1914:pl. 22, figs. 7–11) clearly has a dorsal median depression and all six specimens of this species collected by the present author have a flattening or slight sulcus in the brachial valve, thus blurring the distinction between *poststriatula* and *Schizophoria swallovi* (Hall).

Distribution.—This description is based on collections from localities SL392 (8 specimens), and SL394 (5 specimens).

Order Strophomenida Öpik
Suborder Strophomenidina Öpik
Superfamily Strophomenacea King
Family Leptaenidae Hall and Clarke
Genus ***Leptagonia*** M'Coy, 1844

Leptagonia missouriensis Carter, 1968
Figs. 3.24–3.29

?1892 *Leptaena rhomboidalis* (Wilckens): Hall and Clarke, pl. 8, fig. 30, 31.
1894 *Plectambonites rhomboidalis* (Wilckens): Keyes, pl. 39, fig. 6.
.1909 *Leptaena rhomboidalis* (Wilckens): Weller, p. 292, pl. 12, fig. 3 (not fig. 2).

.1914 *Leptaena analoga* (Phillips): Weller, p. 49, pl. 2, fig. 3, 4 (not fig. 1, 2, 5–10).
.1938*a* *Leptaena analoga* (Philips) De Koninck: Branson, p. 24–26, 161, pl. 5, fig. 31; pl. 17, fig. 11, 12.
v.1944 *Leptaena analoga* (Phillips): Branson, pl. 31, fig. 11, 12.
.1961 *Leptaena analoga* (Phillips): Nelson, pl. 4, fig. 26.
v*1968 *Leptagonia missouriensis* Carter, p. 1142–1143, pl. 148, fig. 1–14.
v.1987 *Leptagonia missouriensis* Carter: Carter, p. 21, pl. 1, fig. 11–15.

Holotype.—University of Illinois RX-144, from the "white chert" beds of the lower Burlington Limestone at Louisiana, Pike County, Missouri.

Diagnosis.—Small- to medium-sized subquadrate *Leptagonia* with small subangular ears, moderately coarse irregular rugae on the visceral disc of the pedicle valve, a flat or slightly concave dorsal visceral disc, and with the ventral trail distinctly defined by an enlarged ruga.

Remarks.—It now appears that this species first occurs in the Glen Park Limestone and becomes extinct somewhere within the lower Burlington Limestone, ranging throughout the Kinderhookian and early Valmeyeran of the midcontinent. It is readily differentiated from the larger form more commonly referred to *Leptaena analoga* (Phillips) by American authors by its smaller size, small ears, fewer more irregular rugae, and subquadrate outline. The larger species first occurs in the Chouteau Limestone and, like *L. missouriensis,* ranges into the lower Burlington Limestone. Both species occur together in the Fern Glen Formation and lower Burlington Limestone of eastern Missouri.

Brunton (1968:21–31) recently redescribed the type species of *Leptagonia, L. analoga* (Phillips), and rediagnosed the genus as having a prominent pseudospondylium in the pedicle valve and a raised adductor platform in the brachial valve. The latter structure does not seem to be as well developed in North American species of this genus as was illustrated and described by Brunton. Good interiors of Glen Park specimens are not available for study at present.

Distribution.—In the Glen Park Formation this species has been found only at locality SL393 (13 specimens).

Suborder Orthotetidina Waagen
Superfamily Orthotetacea Waagen
Family Schuchertellidae Williams
Subfamily Schuchertellinae Williams
Genus **Schuchertella** Girty, 1904

Table 5.—*Measurements (in mm) of the types of* Schuchertella hardinensis, *new species.*

Specimen no.	Locality	Length	Width
	Pedicle valves		
CM 34628	SL396	23.3	31.2
CM 34629	SL396	24.5	±33.4
IGS 80P9	SL393	+17.2	+25.1
	Brachial valves		
CM 34630	SL396	16.0	23.3
CM 34631	SL396	17.5	22.4
CM 34632	SL396	15.1	18.5
IGS 80P8	SL393	16.0	+26.0
CM 34633	SL393	12.2	+16.6
CM 34634	SL393	10.0	11.6

Schuchertella hardinensis, new species
Fig. 3.30–3.41

v.1906 *Orthothetes chemungensis* (Conrad): Weller, p. 440, pl. 6, fig. 5, 6.
v.1914 *Schuchertella* sp.: Weller, pl. 7, fig. 9, 10.

Holotype.—CM 34628, Fig. 3.30, 3.32. Collected by the author at locality SL396, April 1986.

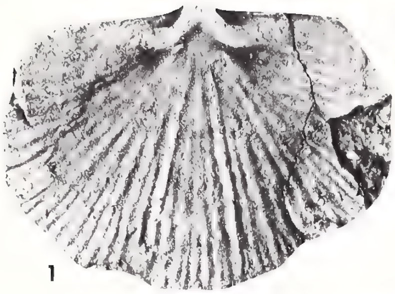
Paratypes.—CM 34629–34632, Fig. 3.31, 3.33–3.37, same collection as the holotype; IGS 80P8, 80P9, from locality SL393, collected by C. Collinson; CM 34633, 34634, from SL393, collected by the author, 1985.

Description.—Medium size for genus, weakly convexo-concave; outline highly variable from transversely subquadrate to almost subelliptical; greatest width usually attained near midlength; body cavity thin to moderately thick; ornament finely and evenly costellate, new costellae randomly added by intercalation in all growth stages in both valves; intercostal furrows with very fine closely and regularly spaced posteriorly convex growth lines; strong growth varices irregularly spaced.

Pedicle valve thin, variable in profile from weakly convex to weakly resupinate; cardinal extremities rounded to slightly subangular; beak very small with no indication of cementation observed; ventral interarea weakly apsacline to almost catacline, low, acutely triangular; pseudodeltidium moderately convex, about as wide as high; dental plates lacking, other internal details not observed.

Brachial valve thicker than pedicle valve, moderately to strongly inflated, often asymmetrical in shape and outline, usually most convex in umbonal region; cardinal extremities rounded; dorsal interarea very low, acutely triangular, anacline; narrow chilidium covering base of low bilobed cardinal process; other internal details not observed.

Distinguishing characters.—This species is characterized by its rounded to slightly subangular cardinal extremities, finely and regularly costellate ornament, and moderately to strongly convex brachial valve.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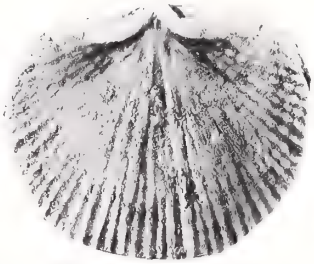
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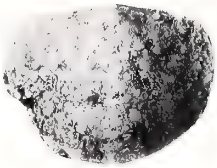
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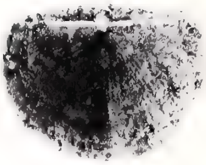
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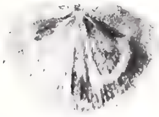
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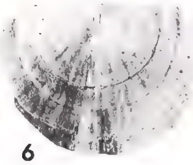
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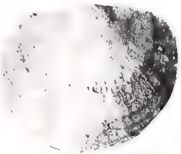
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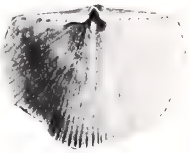
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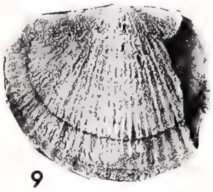
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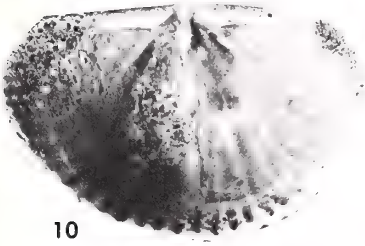
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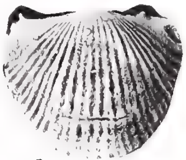
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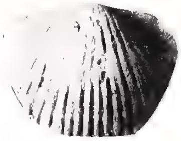
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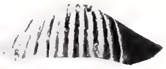
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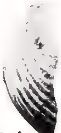
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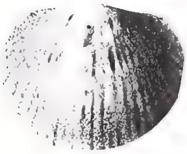
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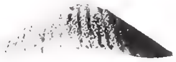
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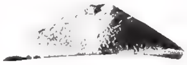
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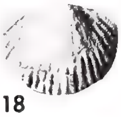
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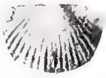
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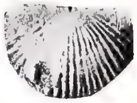
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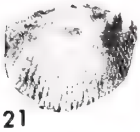
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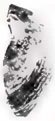
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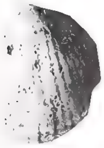
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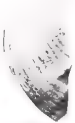
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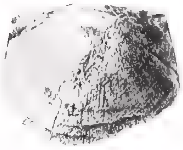
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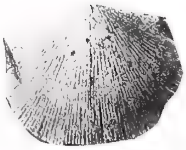
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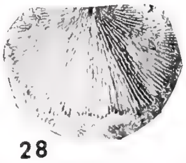
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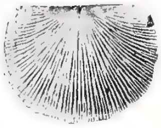
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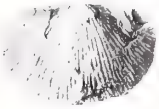
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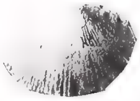
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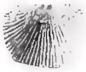
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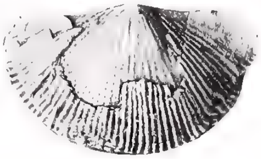
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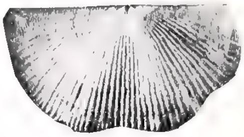
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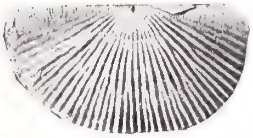
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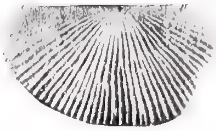
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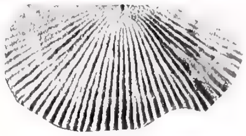
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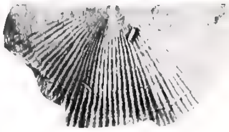
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Remarks.—Weller (1906:440) first assigned specimens of *Schuchertella hardinensis* n. sp. from the type Glen Park to the commonly identified Devonian species, *Schuchertella chemungensis* (Conrad), then (1914:pl. 7, fig. 9, 10) referred to the same specimens as *Schuchertella* sp. The rounded to subangular cardinal extremities and inflated brachial valve serve to distinguish *Schuchertella hardinensis* n. sp. from both the Chemung species and *Schuchertella lens* (White), the type species of the genus, from the Louisiana Limestone.

The brachial valve referred to *Schuchertella rubra* Weller by Branson (1938*a*:161, pl. 17, fig. 26) from the "Bushberg" Sandstone is similar in outline and ornamentation to *Schuchertella hardinensis* n. sp. However, the specimen is almost flat, an unusual condition in any Mississippian orthotetid.

Branson also described a new schellwienellid, *Schellwienella bushbergensis,* based on a single specimen from the same unit, distinguishing it from the other orthotetid specimens in his collection by its serrate ornamentation and inflated umbonal region. This species may prove to belong in the genus *Serratocrista* Brunton, 1968, and its relationship to *Schuchertella hardinensis* n. sp. is unclear. It is much larger than most of the brachial valves from the Glen Park. The unusual serrate costellae of the Bushberg form may reflect superior preservation rather than morphological differences. Unfortunately, additional "Bushberg" specimens from Branson's seemingly lost locality are needed to adequately characterize Branson's species.

Distribution.—This species is fairly common at most Glen Park localities, although good specimens are difficult to obtain. It is conspicuously absent in the typically silty dolomitic facies of Pike County, Illinois, but occurs in small numbers in the micritic limestone at SL393 (6 specimens). In Calhoun County, it occurs commonly in the oolitic facies at SL395 (4 specimens) and SL396 (27 specimens). Two specimens are in the IGS collection from Jerseyville Hollow, Jersey County, and it is very common at the type Glen Park (36 specimens), SL397, Jefferson County, Missouri.

Suborder Chonetidina Muir-Wood
Superfamily Chonetacea Bronn
Family Anopliidae Muir-Wood
Subfamily Tornquistiinae Afanasjeva
Genus ***Subglobosochonetes*** Afanasjeva, 1976

Subglobosochonetes jerseyensis, new species

Fig. 4.1–4.9

v.1906 *Chonetes* sp. undet.: Weller, p. 441, pl. 6, fig. 8–12.
v.1914 *Chonetes* sp.: Weller, pl. 8, fig. 50, 51, 53–55.

Holotype.—Fig. 4.8, CM 34636, collected by the author, April 1986, from SL397, the type section of the Glen Park Formation, Jefferson County, Missouri.

Paratypes.—Fig. 4.1–4.4, 4.9, IGS 80P10–80P13, collected by T. Gillette, 1942, from the "Hamburg" of Jerseyville Hollow, Jersey County, Illinois. Fig. 4.5, 4.6, FMNH UC11354 (4 specimens, not the specimen figured by Weller, 1914, pl. 8, fig. 52, referred here to *Chonetes glenparkensis* Weller); all collected by S. Weller from the Glen Park Formation at the type section, Jefferson County, MO, SL397. Fig. 4.7, CM 34635, collected by the author, April 1986, SL397.

Description.—Medium size for genus, moderately concavo-convex, transversely subovate in outline; maximum width attained at hingeline in subadult specimens, but posterior to mid-length in fully adult specimens with subangular cardinal extremities; ears small, defined by moderately concave flexures on ped-

←

Fig. 4.—Chonetids. 4.1–4.9, *Subglobosochonetes jerseyensis* n. sp.; 4.1, 4.2, brachial valve interiors from SL511, IGS 80P10 and 80P11, ×6; 4.3, 4.4, ventral and dorsal views of a complete shell from SL511, IGS 80P12, ×3; 4.5, 4.6, a brachial valve interior and a brachial valve exterior from SL397, FMNH UC11354, ×3; 4.7, a pedicle valve exterior from SL397, CM 34635, ×3; 4.8, the holotype, a pedicle valve interior from SL397 showing hingeline spine distribution, CM 34636, ×3; 4.9, a large pedicle valve from SL511 showing the irregular ribbing, IGS 80P13, ×3. 4.10–4.25, *Plicochonetes? glenparkensis* (Weller); 4.10, 4.15–4.17, interior (×6), ventral, anterior and posterior views of a large pedicle valve topotype from SL397, CM 34637, ×3; 4.11, a large pedicle valve with a pair of hinge spines preserved from SL395, CM 34638, ×3; 4.12–4.14, ventral, anterior and lateral views of the holotype from SL397, FMNH UC11355, ×3; 4.18–4.23, two small pedicle valves, a small brachial valve external mold and three views of a slightly larger pedicle valve from SL392, CM 34639–34642, ×3; 4.24, 4.25, ventral and lateral views of an elongate abraded specimen from SL397, illustrated by Weller as *Chonetes* sp. (1914: pl. 8, fig. 52), FMNH UC11354, ×3. 4.26–4.32, *Rugosochonetes* cf. *C. gregarius* (Weller); 4.26–4.29, two large pedicle valves and molds of two brachial valve exteriors from SL392, CM 34643–34646, ×3; 4.30–4.32, two small pedicle valves and a small brachial valve exterior from SL393, IGS 80P14–80P16, ×3. 4.33–4.38, *Rugosochonetes pikensis* n. sp.; 4.33, a pedicle valve, the holotype, IGS 80P17; 4.34–4.37, four molds of brachial valve exteriors, IGS 80P18–80P21; 4.38, a brachial valve exterior, IGS 80P22, all from SL393, all ×3.

Table 6.—*Measurements (in mm) of the types of* Subglobosochonetes jerseyensis, *new species.*

Specimen no.	Locality	Length	Width	Height
Pedicle valves				
IGS 80P13	SL511	8.0	±10.6	3.2
IGS 80P12	SL511	7.1	9.4	2.3
CM 34636	SL397	6.8	8.4	1.8
CM 34635	SL397	6.4	8.3	—
Brachial valves				
IGS 80P10	SL511	6.8	9.0	—
IGS 80P11	SL511	5.9	6.9	—
FMNH UC11354	SL397	6.6	9.3	—
FMNH UC11354	SL397	5.5	7.2	—

Table 7.—*Measurements (in mm) of the types of* Rugosochonetes pikensis, *new species.*

Specimen no.	Locality	Length	Width	Height
Pedicle valve (holotype)				
IGS 80P17	SL393	6.8	11.1	2.6
Brachial valves				
IGS 80P18	SL393	5.7	10.7	—
IGS 80P19	SL393	5.8	10.7	—
IGS 80P20	SL393	5.4	9.6	—
IGS 80P21	SL393	5.9	11.0	—
IGS 80P22	SL393	5.6	10.6	—

icle valve and large triangular antero-lateral flattened areas on brachial valve; ornament of both valves consisting of fine capillae which increase by both bifurcation and intercalation, producing an irregularly ribbed appearance (ribbing often obscured by effects of postmortem abrasion); strong growth varices irregularly spaced on both valves; growth lines not observed.

Pedicle valve moderately convex in both lateral and anterior profile, slightly arched medially, most convex in umbonal region; flanks sloping evenly to antero-lateral margins; ears slightly compressed; beak inconspicuous; five pairs of spine bases along cardinal margin in holotype (Fig. 4.8); angle of spines not determined; ventral interarea low, slightly concave, apsacline to nearly orthocline; tiny pseudodeltidium present; interior with short, stout median septum, small broad teeth, five pairs of fine spine perforations under the ventral interarea and directed medially; muscle scars faint and separated by a low median ridge; inner antero-lateral surface capillate reflecting external ornamentation with fine papillae on crests of capillae.

Brachial valve weakly concave, antero-medially flattened at auriculations; dorsal interarea very low, inconspicuous, hypercline; chilidial plates not observed; interior with short bilobed cardinal process supported only by stout inner socket ridges; alveolus moderately developed; anderidea widely divergent, not connected to socket ridges; one prominent pair of accessory septa present with radially arranged endospines coalescing to form several fainter pairs of septa in antero-medial portion of valve; brachial ridges well defined in some specimens (see Fig. 4.5); muscle scars not observed.

Distinguished characters.—This species can be differentiated by its subovate outline, moderate convexity, irregular ribbing consisting of fine capillae that increase by both bifurcation and intercalation on both valves, the maximum width is attained anterior to the hingeline in adult specimens, and five pairs of fine spines.

Remarks.—*Subglobosochonetes jerseyensis* n. sp. is not similar to other chonetid species in the Glen Park Limestone or other Kinderhookian formations in the midcontinent. It is most similar to *Subglobosochonetes norquayensis* Carter, 1987, from the Banff Formation of Alberta of late Kinderhookian age. It differs from the latter in its much less inflated profile and different ribbing patterns. In *Subglobosochonetes jerseyensis* n. sp. the capillae increase by both bifurcation and intercalation in both valves, whereas in *S. norquayensis* the capillae increase by bifurcation in the pedicle valve and by intercalation in the brachial valve.

Subglobosochonetes malevkensis (Sokolskaya), the type species from the Tournaisian of the Soviet Union, has stronger ribbing, is widest at the hingeline, and has fewer spines. Internally, the Soviet species has weaker accessory septa and less divergent anderidea.

Distribution.—This species has been found at the following Glen Park Formation localities: SL397 (17 specimens in CM, 4 specimens FMNH, Weller Coll.); Jerseyville Hollow, Jersey County, IL, Gillette Coll. (16 specimens). Both collections are from the oolitic facies of the Glen Park.

Family Rugosochonetidae Muir-Wood
Subfamily Rugosochonetinae Muir-Wood
Genus ***Rugosochonetes*** Sokolskaya, 1950

Rugosochonetes pikensis, new species
Fig. 4.33–4.38

Holotype.—A pedicle valve, Fig. 4.33, IGS 80P17, collected by C. Collinson from SL393.

Paratypes.—Five brachial valves, Fig. 4.34–4.38, IGS 80P18–80P22, same collection as holotype.

Description.—Small to medium for genus, strongly concavo-convex for genus, much wider than long; outline transversely semicircular to tranversely subquadrate; cardinal extremities subangular to subrounded, greatest width usually attained anterior to hingeline, usually in posterior third of valve; body cavity thin; ornament consisting of about 9–10 sharp, coarse capillae per 3 mm near mid-anterior margin with weak, irregularly spaced growth varices and very fine closely spaced growth lines; capillae increase mainly by bifurcation on both valves, very rarely by intercalation.

Pedicle valve strongly convex, most inflated in umbonal region, medially and evenly arched, ears smooth and delimited by concave flexures, flanks sloping evenly to antero-lateral margins; no sulcus in any specimen observed; beak inconspicuous; cardinal margins straight with two pairs of spine bases, angle of spine inclination not determinable; ventral interarea and interior details not observed.

Brachial valve moderately concave with weak median fold and two weak lateral sulci; cardinal extremities smooth or with very faint capillae; protegulal node narrow and elongate; dorsal interarea, if present, not observed; cardinal process small, bilobed; large, deep alveolus present; moderately long, slightly divergent anderidea not attached to cardinal process or inner socket ridges; brachial ridges present but presence of median septum not determinable; endospines radially aligned; other internal details not observed.

Distinguishing characters.—This species is characterized by its strongly capillate ornament, transverse outline with greatest width anterior to the hingeline, inflated evenly convex pedicle valve, moderately concave brachial valve with a weak medial fold and two weak lateral sulci.

Remarks.—Assignment of this new species to the genus *Rugosochonetes* Sokolskaya is based primarily on outline, the strongly capillate ornament, the presence of folding on the brachial valve, and the presence of a large, deep alveolus and brachial ridges in the brachial valve. Few pedicle valves are available for study and the exact number and inclination of the hinge spines is not determinable, nor is the presence of a long median septum in the brachial valve.

Rugosochonetes pikensis n. sp. is not similar to the other three species of chonetids in the Glen Park Formation. In rocks of this age, only *Chonetes alatus* Moore, 1928, from the English River Sandstone and "*Chonetes* bed" of Iowa and northern Illinois is similar in size and ornamentation to *Rugosochonetes pikensis* n. sp. It differs in having an extended hingeline, a weak ventral sulcus, and an evenly concave medial portion of the brachial valve.

Distribution.—This description is based on a single collection of 19 specimens, all disarticulated valves, from locality SL393.

***Rugosochonetes* cf. *Chonetes gregarius* Weller, 1901**
Fig. 4.26–4.32

1901 *Chonetes gregarius* Weller, p. 149–150, pl. 12, fig. 2.

Types.—Two syntypes, FMNH UC6654, from Kinderhook Bed 3, Burlington, Iowa, S. Weller Collection.

Referred specimens.—Two pedicle valves and two brachial valves, Fig. 4.26–4.29, CM 34643–34646, from locality SL392, collected by the author; two pedicle valves and one brachial valve, Fig. 4.30–4.32, IGS 80P14–80P16, from locality SL393, collected by C. Collinson.

Table 8.—*Measurements (in mm) of referred specimens of* Rugosochonetes *cf.* Chonetes gregarius *Weller, 1901, from the Glen Park Formation.*

Specimen no.	Locality	Length	Width
Pedicle valves			
CM 34643	SL392	6.7	8.0
CM 34644	SL392	6.2	8.1
IGS 80P14	SL393	4.6	7.1
IGS 80P15	SL393	4.2	6.1
Brachial valves			
CM 34645	SL392	6.5	7.8
CM 34646	SL392	5.1	7.1
IGS 80P16	SL393	3.0	4.1

Description of Glen Park specimens.—Small to medium for genus, moderately to strongly concavo-convex, outline semicircular to subquadrate; cardinal extremities subangular with greatest width attained anterior to hingeline, usually in posterior third of valve; body cavity thin; ornament consisting of about 20–23 fine capillae per 3 mm near anterior margin in large specimens, rare coarse growth varices, and regularly spaced growth lines that appear only on crests of capillae giving them crenulate appearance; ribbing increases by bifurcation on pedicle valve and by both bifurcation and more rare intercalation on brachial valve.

Pedicle valve moderately to strongly inflated, most convex medially, flanks evenly convex except for slightly compressed cardinal extremities; beak tiny, inconspicuous; cardinal margins diverging a few degrees from horizontal in large specimens, straight in small specimens; three or more pairs of spines at cardinal margins, inclined at high angle of 60 degrees or more; ventral interarea low, slightly apsacline to almost orthocline; delthyrium and pseudodeltidium not observed; interior not observed.

Brachial valve thin and weakly concave, cardinal extremities slightly flattened and poorly defined by slight flexures; cardinal margins straight, dorsal interarea not observed; small elongate protegulal node well defined; cardinal process small, bilobed with small alveolus; inner socket ridges diverging from hingeline; median septum extending anteriorly to about midlength; anderidea slightly raised; endospines arranged in radial rows; other internal details not observed.

Remarks.—These Glen Park Formation specimens are compared with the poorly known Early Kinderhookian chonetid species *Rugosochonetes gregarius* (Weller), described from "Bed 3"at Burlington, Iowa. "Bed 3" usually consists of two thin beds, the lower one an "impure" limestone with numerous small chonetids, and an upper oolitic bed. It is possible that "Bed 3" is a northern extension of the Glen Park Limestone. In any case the stratigraphic position and lithologic similarity of the two

Table 9.—*Measurements (in mm) of types and referred specimens of* Plicochonetes? glenparkensis *(Weller).*

Specimen no.	Locality	Length	Width	Height
	Pedicle valves			
Holotype				
FMNH UC11355	SL397	6.4	8.0	3.0
CM 34638	SL395	6.7	8.3	2.9
CM 34637	SL397	6.7	8.3	2.6
CM 34639	SL392	4.3	5.5	1.6
CM 34640	SL392	3.1	4.7	1.3
CM 34642	SL392	5.0	6.0	3.0
FMNH UC11354	SL397	6.5	7.2	3.1
	Brachial valve			
CM 34641	SL392	4.2	5.8	—

widely separated units invites comparison of several faunal elements. These Glen Park specimens agree in size, outline, convexity, and general proportions of the Iowa species. The differences between the two are subtle but persistent. The Glen Park specimens have about 20–23 capillae per 3 mm at the anterior margin, and the capillae increase only by means of bifurcation on the pedicle valve. Conversely, the Iowa specimens seem to have slightly finer capillae and the ventral capillae apparently increase both by bifurcation and intercalation. The dorsal interarea of the Iowa species is largely unknown.

Distribution.—*Rugosochonetes* cf. *gregarius* (Weller) has been found at the following localities: SL392 (24 specimens), SL393 (16 specimens), and SL394 (4 specimens).

Subfamily Plicochonetinae Sokolskaya
Genus ***Plicochonetes*** Paeckelmann, 1930

Plicochonetes? glenparkensis (Weller, 1906)
Fig. 4.10–4.25

v*1906 *Chonetes glenparkensis* Weller, p. 441, pl. 6, fig. 7.
v1914 *Chonetes glenparkensis* Weller: Weller, pl. 8, fig. 30 (*not* fig. 47–49).
v.1914 *Chonetes* sp.: Weller, pl. 8, fig. 52.
v.1938*a* *Chonetes ornatus* Shumard: Branson, p. 132, 133, pl. 16, fig. 14.

Holotype.—Fig. 4.12–4.14, FMNH UC11355, collected by S. Weller from SL397.

Description.—Small for genus, strongly concavo-convex with arched venter; outline transversely subovate to almost subcircular in adult specimens, transversely semicircular to transversely subelliptical in immature specimens; cardinal extremities small, subangular to subrounded; greatest width attained anterior to hingeline in posterior third of valve; ornament consisting of about 7–10 fine costellae per 3 mm at anterior margin or total of about 27 to 45 costellae on entire shell (holotype with 7–8 costellae per 3 mm or total of 27 costellae), crossed by fine regular growth lines which give crenulate appearance when spalled or worn; costellae increase by bifurcation on pedicle valve and by both bifurcation and intercalation on brachial valve; costellae becoming very faint or absent at cardinal extremities of both valves.

Pedicle valve strongly convex with arched venter, most convex in umbonal region, sloping evenly to antero-lateral margins; ears small, compressed, delineated by concave flexures; beak small, slightly overhanging hingeline; cardinal margins nearly straight or diverging slightly from horizontal, lacking spines entirely in holotype or with one pair of spines as in Fig. 4.11; angle of spine inclination, when present, not determined; ventral interarea low, orthocline; delthyrium wider than long, partially occluded by small pseudodeltidium; teeth broad; median septum short and stout with low median ridge extending almost to anterior margin; endospines lacking in visceral region, arranged in radial rows near margins and at cardinal extremities; other internal details not observed.

Brachial valve moderately concave with flattened cardinal extremities; small elongate protegulal node present at center of hingeline; interarea not observed; interior not known.

Distinguishing characters.—*Plicochonetes? glenparkensis* (Weller) is characterized by its coarse ornamentation of from about 7–10 fine costellae per 3 mm at the anterior margin, small cardinal extremities, narrow hingeline, poor development (or lack) of spines on the hingeline, and orthocline ventral interarea.

Remarks.—Weller (1914:87–89) interpreted his Glen Park species as being identical with a not very similar chonetid found in the Chouteau Limestone of middle Kinderhookian age. As a consequence, his description and means of differentiating the species was based primarily on Chouteau Limestone specimens.

Weller misinterpreted the rounded cardinal extremities of the holotype to signify that the specimen was abraded and originally much wider in the hingeline than is now seen. He failed to recognize the specimen figured here, Fig. 4.24, as belonging to *Plicochonetes? glenparkensis.* This specimen is probably the one he referred to as a separate chonetid species in his original Glen Park paper (1906: 442). The latter is indeed water worn, but the costellae and growth lines are readily observed under water and indicate that the specimen clearly is assignable to *P. glenparkensis.*

This writer has recently recovered a well preserved pedicle valve, also from the type Glen Park, as illustrated on Fig. 4.15–4.17. This specimen confirms the narrow hingeline, small ears, and lack of hingeline spines seen in the holotype. In addition, a rare specimen of this species was found at locality SL395 in Hamburg, Calhoun County, Illinois. This well preserved pedicle valve has a pair of hinge spine bases preserved but agrees in every other respect with the holotype and other specimens from the type Glen Park, Jefferson County, Missouri.

Weller's misapplication of the name *glenparkensis* to the Chouteau specimens has resulted in a misunderstanding of the true nature of the species. Unfortunately, his interpretation has been followed by many subsequent workers. The species name has been incorrectly applied to various taxa which are unrelated to *Plicochonetes? glenparkensis* (Weller) from many horizons and localities in North America and the Soviet Union.

Weller (1914:88) suggested that the taxon he interpreted as *Chonetes glenparkensis,* based on the Chouteau specimens, was probably

> . . . most closely allied to *C. logani,* and has sometimes been so identified, but it may be distinguished by its greater size, although some examples of *C. logani* are fully as large as any example of *C. glenparkensis,* by the greater extension of the hinge-line and more conspicuous auriculations of the shell, and by the somewhat coarser costae separated by proportionally wider intercostal furrows.

The present writer pointed out (1968:1144) the likelihood that most Chouteau specimens referred to *Chonetes glenparkensis* should be assigned to *Caenanoplia logani* (Norwood and Pratten).

Branson (1938*a*) mistakenly assigned this species to *Chonetes ornatus* Shumard, assuming that *Plicochonetes? glenparkensis* (Weller) actually included the Chouteau species which have large auriculations.

Plicochonetes? glenparkensis (Weller) is not similar to most other Lower Mississippian North American chonetid species. It can be distinguished from *Plicochonetes ornatus* (Shumard) from the underlying late Famennian Louisiana Limestone by the latter's wider hingeline, larger auriculations, slightly coarser costellae, and intercalation of ribbing on the brachial valve. *Plicochonetes canadensis* Carter, 1987, from the Banff Formation of Alberta has much larger wider auriculations and much finer ribbing than does *Plicochonetes? glenparkensis* (Weller).

Assignment of *Chonetes glenparkensis* Weller to the genus *Plicochonetes* Paeckelmann is tentative because this genus presumably is partially characterized by large auriculations (Muir-Wood, 1962: 82) and a septum in both valves. *Plicochonetes? glenparkensis* (Weller) has small auriculations in mature specimens, although they are relatively much larger compared to the visceral disc in immature specimens. Furthermore the presence of a dorsal median septum has not been demonstrated in *Plicochonetes? glenparkensis* (Weller).

Distribution.—This species is extremely rare at the topotype locality, SL397. Weller's collections contain the holotype and the other Weller specimen figured here (Fig. 4.24), both pedicle valves. Despite extensive collecting at this locality this writer found only one other specimen, the pedicle valve illustrated here as Fig. 4.15–4.17. Six pedicle valves were collected by the writer at SL395, in Hamburg, Calhoun County, Illinois, from the so-called Hamburg Oolite. These specimens are authentic in every respect and compare closely with the holotype. Several collections of much smaller specimens are provisionally assigned to this species: SL392 (6 specimens), SL393 (23 specimens), SL394 (2 specimens), and an IGS collection from Gresham Hollow (3 specimens). If all of these collections are correctly identified, the species is present, but rare, over nearly the entire area of distribution of the Glen Park Formation.

Suborder Productidina Waagen
Superfamily Productacea Gray
Family Productellidae Schuchert
Subfamily Productellinae Schuchert
Genus ***Orbinaria*** Muir-Wood and Cooper, 1960

Orbinaria? brownensis, new species
Fig. 6.11–6.16

Holotype.—A pedicle valve, Fig. 6.11–6.12, IGS 80P27, collected by C. Collinson from locality SL393, Pike County, Illinois.

Paratypes.—Fig. 6.13–6.16, IGS 80P28–80P30, same collection as the holotype.

Description.—Small for genus, moderately concavo-convex, length-width ratio variable but usually wider than long in larger shells; body cavity thin; cardinal extremities subangular to subrounded; outline transversely subquadrate to subovate; hingeline slightly shorter than greatest width, which is usually attained at about midlength; cardinal extremities forming small auriculations.

Pedicle valve moderately convex, greatest convexity in umbonal region; venter slightly arched, flanks sloping evenly to antero-lateral margins; auriculations moderately well defined by concave flexures, slightly compressed; beak small, slightly overhanging hingeline, with small cicatrix on some specimens; ornament consisting of numerous irregular rugae and numerous scattered slightly elongate spine ridges which may be crudely arranged in quincunx in some specimens; growth lines sinuous, irregular, slightly lamellose; spines very fine, probably nearly erect, occurring at anterior terminations of spine ridges and slightly more densely on auriculations and near hingeline; interarea, if present, not observed; internal details not observed.

Brachial valve moderately and evenly concave except at car-

Table 10.—*Measurements (in mm) of the types of* Orbinaria? brownensis, *new species.*

Specimen no.	Locality	Length	Width	Height
		Pedicle valves		
IGS 80P27	SL393	9.9	13.3	3.8
IGS 80P28	SL393	8.5	9.0	2.5
IGS 80P29	SL393	5.2	7.8	2.4
		Brachial valve		
IGS 80P30	SL393	7.7	9.3	—

dinal extremities which are delimited by slightly flattened or convex flexures; conspicuous small round protegulal node present at center of hingeline; ornament similar and complementary to that of opposite valve except that rounded dimples reflect elongate spine ridges of pedicle valve and fine spines are very rare; interior not observed.

Distinguishing characters.—This species is characterized by its small size, transversely subquadrate to subovate outline, elongate spine ridges which may be crudely arranged in quincunx on the pedicle valve, and rounded dimples in the brachial valve.

Remarks.—*Orbinaria? brownensis* n. sp. is tentatively assigned to the genus *Orbinaria* Muir-Wood and Cooper on the basis of its external shape and ornamentation. However, there are some significant differences between this new species and *Orbinaria pyxidata* (Hall), the type species from the Louisiana Limestone. *Orbinaria pyxidata* is much larger, much more inflated, lacks a cicatrix, and has a distinct row of spines at the hingeline. In addition, the dorsal dimples are elongate, not rounded, and Muir-Wood and Cooper (1960:149) state that dorsal spines are lacking, although there do seem to be fine spines on Plate 35, figure 10 of their book.

Distribution.—This description is based on a single collection of 16 specimens from locality SL393.

Subfamily Chonopectinae Muir-Wood and Cooper

Ruthiphiala, new genus

Fig. 5.1–5.12, 6.1–6.10

Type species.—*Pustula bushbergensis* Branson, 1938, from the "Bushberg Sandstone" of Montgomery County, Missouri, of early Kinderhookian age.

Other assigned species.—*Productella sublaevis* Weller, 1914, originally described from the English River Sandstone Member of the Hannibal Formation at Kinderhook, Pike County, Illinois. Specimens of this species from the Glen Park Formation, SL393, are described below.

Table 11.—*Measurements (in mm) of the types of* Ruthiphiala sublaevis *(Weller, 1914).*

Specimen no.	Locality	Length	Width	Height
	Pedicle valves			
Lectotype				
FMNH UC10558	Kinderhook, Illinois	25.6	34.0	9.0
IGS 80P25	SL393	21.6	29.5	4.8
	Brachial valves			
Paralectotype				
FMNH UC10558	Kinderhook, Illinois	32.7	41.4	10.7
IGS 80P23	SL393	29.8	37.9	10.1
IGS 80P24	SL393	26.7	32.3	7.3
IGS 80P26	SL393	24.3	32.5	5.0

Derivation of name.—Ruth, a woman's name, from the latin *phiala,* a saucer or bowl.

Diagnosis.—medium sized moderately concavo-convex chonopectinids with weakly expressed ornamentation consisting only of fine elongate spine ridges, crudely arranged in quincunx, bearing very fine prostrate spines at their anterior terminations, a row of coarse laterally inclined spines on the ventral hingeline, and very fine sinuous growth lines; spines seemingly lacking on brachial valve; cicatrix very small; ventral interarea short and orthocline, dorsal interarea very short, possibly lacking in some specimens, nearly catacline; dorsal interior with moderately large erect bilobed cardinal process, large deep alveolus, short thin median septum, very fine endospines, tiny sockets, and lacking brachial ridges.

Comparisons.—*Ruthiphiala* differs from most other chonopectinid genera in its lack of concentric rugose ornamentation. In this respect it is most similar to the genera *Chonopectus* Hall and Clarke, 1893, and *Acanthatia* Muir-Wood and Cooper, 1960. *Ruthiphiala* differs from *Chonopectus* in having numerous spine ridges and fine prostrate spines on the pedicle valve, whereas *Chonopectus* lacks ventral spines except at the hingeline. *Ruthiphiala* is most similar to the Late Devonian genus *Acanthatia* and can be differentiated by its elongate spine ridges and fine prostrate spines on the pedicle valve and its laterally directed hinge spines. *Acanthatia* lacks elongate spine ridges and has more numerous and higher angled hinge spines.

Stratigraphic range.—As presently known this genus seems to be confined to rocks of earliest Carboniferous age.

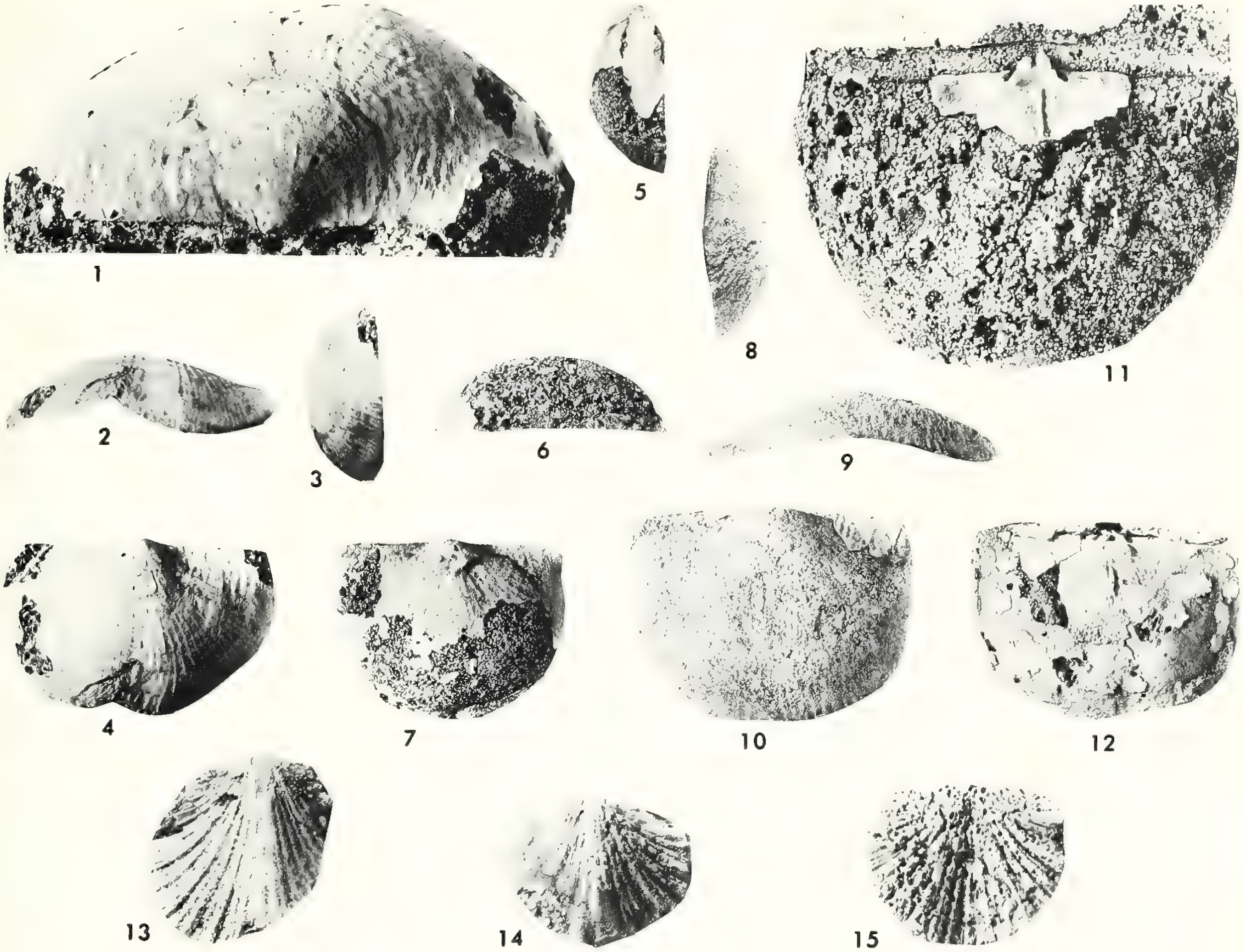


Fig. 5.—Productids and punctate orthids. *Ruthiphiala bushbergensis* (Branson), type specimens; 5.1–5.4, posterior (×2), anterior, lateral and ventral views of the lectotype, UMO 4253; 5.5–5.10, lateral anterior and ventral views of two pedicle valves, paralectotypes UMO 4253 and UMO 3864, respectively; 5.11, mold of brachial valve exterior showing impression of ventral interarea and with cardinalia still preserved, paralectotype UMO 4253; 5.12, nearly complete brachial valve interior, paralectotype UMO 4253; all ×1 except 5.1 and 5.11, ×2; all from "Bushberg" Sandstone float, 7 miles west of Montgomery City, Missouri, collected by E. B. Branson. 5.13–5.15, *Aulacella* n. sp., two pedicle valves and a brachial valve from SL520, CM 34752–34754, all ×5.

Ruthiphiala sublaevis (Weller, 1914)
Fig. 6.1–6.10

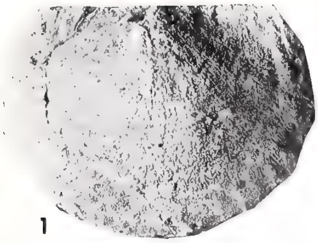
v*1914 *Productella sublaevis* Weller, p. 102–103, pl. 83, fig. 18–20.

Lectotype.—Designated herein, FMNH UC10558, figured by Weller (1914:plate 83, fig. 18, a pedicle valve), from the English River Sandstone at Kinderhook, Pike County, Illinois.

Paralectotypes.—Three specimens, all numbered FMNH UC10558, two specimens figured by Weller (1914:plate 83, fig. 19, a natural cast of a brachial valve interior; fig. 20, a natural mold of a brachial valve exterior). Same collection as the lectotype.

Description.—Medium size for subfamily, semicircular to subovate in outline, wider than long, moderately concavo-convex, non-geniculate; greatest width in adults usually attained at about midlength but immature specimens may reach greatest width at hingeline; auriculations of moderate size, cardinal extremities subangular, delimited by broadly concave flexures; fold and sulcus not developed.

Pedicle valve evenly and moderately convex in both lateral and anterior profile, being most convex near the small beak which projects very slightly beyond hingeline; flanks spreading evenly to antero-lateral margins; interarea not observed; ornament consisting of elongate spine bases over entire valve surface, roughly arranged in quincunx, with very fine spines at anterior terminations of ridges, and with several pairs of coarse hinge spines laterally directed at high angle to hingeline; interior with short median ridge near hingeline and large, radially ridged, moderately impressed ventral muscle field.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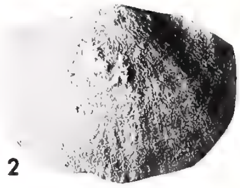
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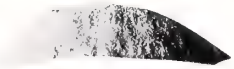
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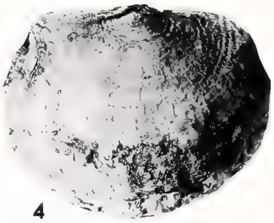
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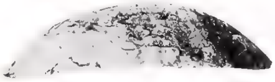
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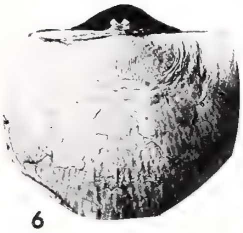
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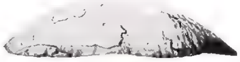
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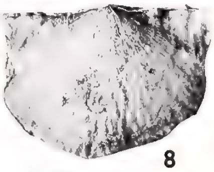
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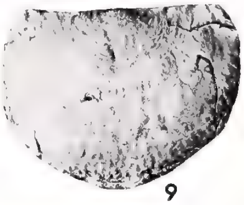
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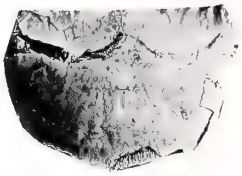
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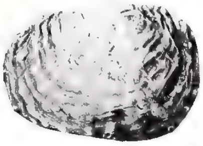
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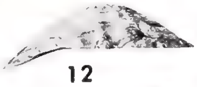
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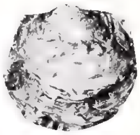
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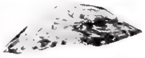
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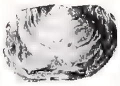
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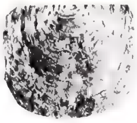
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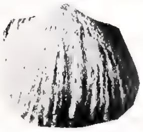
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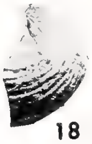
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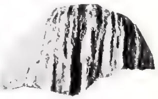
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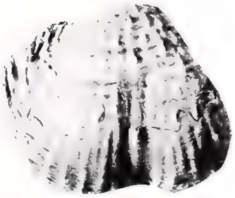
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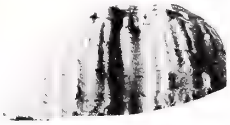
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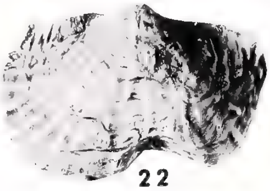
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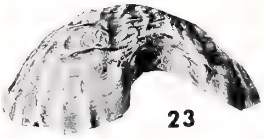
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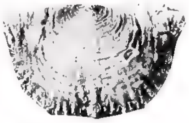
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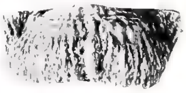
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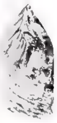
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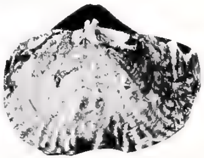
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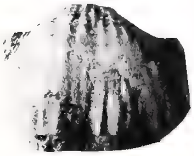
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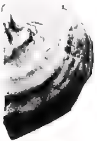
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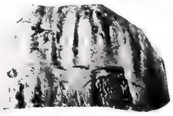
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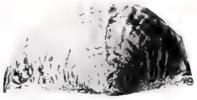
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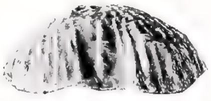
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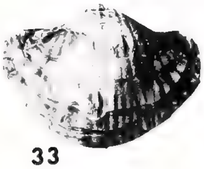
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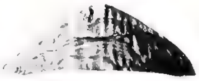
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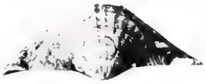
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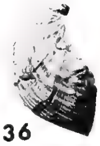
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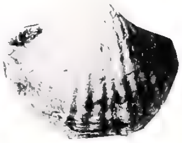
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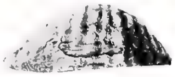
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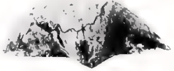
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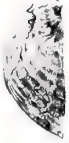
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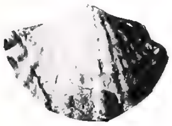
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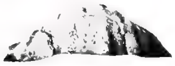
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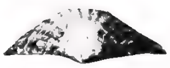
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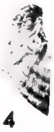
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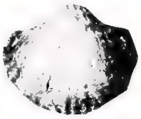
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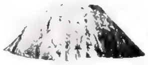
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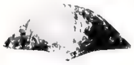
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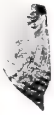
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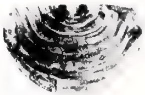
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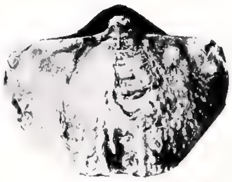
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Brachial valve moderately and evenly concave except for flattened cardinal extremities which are set off by slightly convex flexures, producing thin body cavity; interarea not observed; ornament similar to that of pedicle valve but spines not observed; interior with moderate sized erect bilobed cardinal process with conspicuous alveolus; other internal details not observed.

Distinguishing characters.—This species can be distinguished by its semicircular to subovate outline, relatively narrow hingeline, and short spine ridges arranged in quincunx.

Remarks.—The description of the type species for the genus, *Ruthiphiala bushbergensis* (Branson), was apparently based on only four specimens, two pedicle valve exteriors and two brachial valve interiors. A large pedicle valve, hereby designated the lectotype (Fig. 5.1–5.4), possesses very long spine ridges with fine terminal spine bases. Branson's other figured pedicle valve (Fig. 5.5–5.7) has a nearly complete hingeline preserved with sharply bent dorsally directed lateral auriculations that are smaller but otherwise similar to those seen in the strophalosiid genus *Cyphotalosia* Carter, 1967. The hingeline in this specimen also approximates the maximum width, as do the two brachial valves in the type suite (Fig. 5.11, 5.12). Branson (1938*a*:165) expressed doubts about his species' validity, stating that it might prove to be conspecific with *Ruthiphiala sublaevis* (Weller). Although there is some doubt concerning the exact stratigraphic horizon of Branson's "Bushberg Sandstone," it seems prudent to consider the two names to represent separate taxa because of the morphological differences cited above. The "Bushberg" species is chosen as type species because of the superior preservation of the brachial valve interiors, well preserved exterior ornamention of the pedicle valve, and clear indication of a ventral interarea.

Distribution.—Weller's types came from the lowest Hannibal Formation unit at Kinderhook, Pike County, Illinois, considered by Moore (1928:21) to be the English River Sandstone Member of the Hannibal. The Glen Park Limestone collection is from SL393, also from Pike County, Illinois, and comprises ten specimens.

Genus ***Whidbornella*** Reed, 1943

Whidbornella curtirostra (Winchell, 1865)

Fig. 8.18–8.39

v*1865 *Producta curtirostra* Winchell, p. 114.

1914 *Productus curtirostris* Winchell: Weller, p. 130–131, pl. 14, fig. 8–13.

Lectotype.—Designated herein, a pedicle valve, Fig. 8.18, UMI 1337, White Collection, from the English River Sandstone at Burlington, Iowa.

Paralectotypes.—A natural mold of a brachial valve exterior, Fig. 8.19, 8.20, UMI 1337, from the same collection as the lectotype. Unfigured small slab with a pedicle valve exterior and a natural mold of a brachial valve exterior, UMI 1337, same collection as the lectotype.

Description.—Medium size for genus, moderately concavo-convex; transversely subovate to almost circular in outline; maximum width variable in position from hingeline to mid-length; lateral profile semichordate to subguttate; ears small, subangular, moderately defined, slightly compressed; geniculation poorly developed or not detectable; trails short to moderate; body cavity thin.

Pedicle valve most convex in posterior third of valve, usually near anterior portion of visceral disc, much less convex on trail and flanks; umbonal region broad, very little inflated, produced

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Fig. 6.—Productids. 6.1–6.10, *Ruthiphiala sublaevis* (Weller); 6.1, a natural cast of a brachial valve interior, paralectotype FMNH UC 10558, from the English River Sandstone at Kinderhook, Illinois, Weller Collection; 6.2, 6.3, ventral and anterior views of the lectotype, a pedicle valve, FMNH UC10558, same collection; 6.4–6.7, anterior and ventral views of two natural molds of brachial valve exteriors from SL393 with small amounts of shell matter preserved near the hingeline, showing some of cardinalia, IGS 80P23, 80P24; 6.8, a small pedicle valve from SL393 showing hinge spines, IGS 80P25; 6.9, 6.10, natural mold and exterior of brachial valve from SL393, IGS 80P26, all ×1. 6.11–6.16, *Orbinaria? brownensis* n. sp.; 6.11, 6.12, ventral and anterior views of the holotype, a pedicle valve, IGS 80P27; 6.13, 6.14, ventral and anterior views of a paratype, a pedicle valve, IGS 80P28; 6.15, a small pedicle valve paratype with cicatrix, IGS 80P29; 6.16, a brachial valve exterior paratype, IGS 80P30; all ×2. 6.17–6.32, *Mesoplica? mesicostalis* (Weller); 6.17–6.19, ventral, lateral and anterior views of the lectotype, FMNH UC10585, from the English River Sandstone at Burlington, Iowa, ×1; 6.20–6.23, ventral and anterior views of two pedicle valves from SL393, CM 34647, 34648, ×1.5 (note superior preservation of ornament and pathological deformation of shell in 6.22); 6.24–6.26, dorsal, anterior and lateral views of natural mold of brachial valve exterior from SL393, IGS 80P31, ×1; 6.27, 6.32, dorsal and anterior views of spalled brachial valve interior with cardinal process preserved from SL393, IGS 80P32, ×1; 6.28–6.31, ventral, lateral, posterior and anterior views of a nearly complete pedicle valve from SL393, IGS 80P33, ×1. 6.33–6.50, *Argentiproductus auriculatus* n. sp.; 6.33–6.48, ventral, anterior, posterior and lateral views of four pedicle valves including the holotype, CM 34649 (6.33–6.36) and three paratypes from SL393, CM 34650, 34651 (6.37–6.40, 6.45–6.48), IGS 80P34 (6.41–6.44); 6.49, small brachial valve exterior showing dorsal ornament, IGS 80P35; 6.50, partially spalled brachial valve interior showing cardinal process, IGS 80P36; all from SL393; all ×2 except 6.49, ×4, and 6.50, ×3.

Table 12.—*Measurements (in mm) of types and referred specimens of* Whidbornella curtirostris *(Winchell).*

Specimen no.	Locality	Length	Width	Height	Surface measure
		Pedicle valves			
Lectotype					
UMI 1337	Iowa	25.2	27.7	10.4	31.8
Paralectotype					
UMI 1337	Iowa	19.1	23.8	7.2	22.3
Referred specimens					
IGS 80P41	SL393	27.0	+31.2	11.6	38.0
IGS 80P42	SL393	20.4	25.2	9.6	28.7
IGS 80P43	SL393	20.8	25.3	9.5	29.7
CM 34667	SL393	19.0	25.2	8.9	27.4
		Brachial valves			
Paralectotype					
UMI 1337	Iowa	24.3	+31.5	13.0	33.8
Paralectotype					
UMI 1337	Iowa	17.8	20.2	6.6	19.1
Referred specimens					
CM 34668	SL393	19.9	+26.0	7.7	24.7
IGS 80P44	SL393	24.8	25.8	7.7	31.5

only slightly beyond hingeline; sides of auriculations sharply bent dorsad in lectotype but much less so in paralectotype; beak small; venter evenly convex or slightly arched medially; interarea not observed; visceral disc ornamented with numerous weak irregular rugae best developed on sides of umbonal region, and numerous fine elongate longitudinal spine ridges arranged in quincunx; growth lines very fine and sinuous; anterior to visceral disc spine ridges become much more elongate, simulating irregular costae in some specimens; fine suberect spine bases sparsely scattered on crests of spine ridges, more densely spaced and more or less concentrically arranged near antero-lateral margins; single row of laterally directed fine spines at hingeline; interior with numerous longitudinally arranged fine endospines; muscle field slightly impressed; low ridges forming ear baffles preserved on some specimens; other internal details not observed.

Brachial valve strongly and evenly concave except for ears which are defined by slightly convex flexures, and trail which may be weakly concave or slightly geniculate; dorsal interarea not observed; ornament consisting of numerous weak narrow rugae and numerous fine elongate dimples arranged in quincunx on visceral disc; dimples on trail tend to become much elongated and coalescing to form irregular costae complementary to those of opposite valve; spines apparently lacking; growth lines similar to those of pedicle valve; interior with small sessile bilobed cardinal process with large alveolus, supported by short lateral ridges diverging from hingeline; small elongate antero-laterally directed sockets present on each side of cardinal process; other internal details not observed.

Distinguishing characters.—This species is characterized by its thin body cavity, concentric rugae, and strong radial ornamentation of numerous elongate spine ridges, arranged in quincunx on the visceral disc, that become much elongated anteriorly forming irregular costae on the trail. Internally, the cardinal process has a large alveolus and there are low ridges forming ear baffles in the pedicle valve.

Remarks.—Winchell's types are in the C. E. White Collection at the University of Michigan, UMI 1337, and are from the English River Sandstone at Burlington, Iowa. These specimens are preserved in soft sandstone and lack many taxonomically important morphological characters, such as a good indication of spine distribution and internal details. However, the very close similarity between Winchell's types and the Glen Park collection from locality SL393 leaves little doubt about the specific identity of the two collections. This, in turn, allows a new generic assignment based on the dorsal interiors of the Glen Park specimens.

There are no North American species comparable to *Whidbornella curtirostra* (Winchell). The type species, *Whidbornella caperata* (J. de C. Sowerby), from the Late Devonian of England, as illustrated by Muir-Wood and Cooper (1960:pl. 34, fig. 17–22) and discussed by Reed (1943:71–74), appears to have finer more deeply impressed rugae, weaker less regularly arranged elongate spine ridges on the visceral disc, and the dorsal valve visceral disc is flattened, not evenly and strongly concave as in *Whidbornella curtirostra* (Winchell, 1865).

Distribution.—This species is rare in the English River Sandstone from which it was described. In the Glen Park Formation it occurs only at locality SL393 (60 specimens).

Genus ***Quadratia*** Muir-Wood and Cooper, 1960

Quadratia? sp.

Fig. 8.46

Remarks.—This is the only productoid specimen found by the author at the type section of the Glen Park Formation in Jefferson County, Missouri. It is a small transverse natural mold of a brachial valve. This unique specimen is in no way similar to any other Glen Park productoid, having a flattened visceral disc covered with numerous fine rugae, a few scattered shallow weak dimples, and sinuous growth lines. The postero-medial region is depressed and more strongly convex (concave in a positive sense) and the lateral extremities are weakly reflexed, defining flattened auriculations.

Assignment of this specimen proved to be a perplexing problem, due to a paucity of morphological information. The shape and ornamentation of this specimen are similar to those found in at least three Early Carboniferous productoid genera, all proposed by Muir-Wood and Cooper in 1960, namely *Quadratia, Geniculifera,* and *Rhytiophora. Geniculifera* was rejected as a likely assignment because both valves of that genus tend to be nasute. *Rhytiophora* was rejected because the brachial valves tend to have longer trails and more numerous dorsal dimples. Finally, *Quadratia* has sinuous growth lines similar to those of this specimen, although many productoid genera share this character. Assignment to the genus *Quadratia* is clearly not certain and may have to be revised if more specimens come to light.

Measurements (in mm).—CM 34669, from SL397, length 9.1; width 13.9; height 2.1.

Family Leioproductidae Muir-Wood and Cooper

Subfamily Leioproductinae Muir-Wood and Cooper

Genus ***Mesoplica*** Reed, 1943

Mesoplica? mesicostalis (Weller, 1914)

Fig. 6.17–6.32

v*1914 *Productus mesicostalis* Weller, p. 114, pl. 11, fig. 12–16.

Lectotype.—Designated herein, a pedicle valve, FMNH UC10585, figured by Weller (1914:plate 11, fig. 13–15), from the English River Sandstone at Maple Hill, Washington County, Iowa. Figured herein, Fig. 6.17–6.19.

Paralectotypes.—FMNH UC10585, 6 specimens, 2 figured (Weller, 1914:plate 11, fig. 12, a pedicle valve; fig. 16, an incomplete brachial valve interior), same collection as the lectotype.

Description.—Medium size for family, strongly concavo-convex, transversely subovate to subquadrate in outline; greatest width usually attained anterior to hingeline, often at about mid-length, but specimens with large auriculations may be widest at hingeline; cardinal extremities subangular to subrounded; lateral profile almost semicircular; anterior profile semiovate to subtrapezoidal; body cavity moderately thick; shell substance thin.

Pedicle valve strongly inflated, most convex in umbonal region, otherwise almost evenly curved in profile with flanks dropping steeply to antero-lateral margins, not geniculate; beak small, slightly incurved, umbonal region moderately inflated, extending well posterior to hingeline; small to medium sized auriculations defined by concave flexures; venter flattened anterior to umbonal region, then forming shallow sulcus on trail; ornamentation on visceral disc consisting of weak irregular rugae and narrow elongate quincuncially arranged spine ridges, latter forming irregular costae on trail; sulcus usually with distinctive medial costa larger than those on flanks; spine bases erect, moderately stout, scattered on spine ridges, on auriculations, and near hingeline, those on median costa being larger in diameter than those elsewhere; interior not observed.

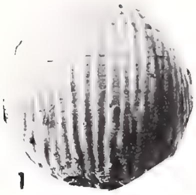
Table 13.—*Measurements (in mm) of types and referred specimens of* Mesoplica? mesicostalis *(Weller, 1914).*

Specimen no.	Locality	Length	Width	Height
		Pedicle valves		
Lectotype				
FMNH UC10585	Iowa	17.1	21.5	11.3
Paralectotypes				
FMNH UC10585	Iowa	18.4	22.8	11.5
FMNH UC10585	Iowa	18.5	+23.3	11.5
FMNH UC10585	Iowa	18.4	20.5	13.7
FMNH UC10585	Iowa	19.6	20.1	14.4
IGS 80P33	SL393	19.9	26.1	12.4
CM 34647	SL393	17.0	±25.8	9.4
CM 34648	SL393	16.9	24.5	7.9
		Brachial valves		
FMNH UC10585	Iowa	17.7	21.9	8.4
IGS 80P31	SL393	15.5	25.4	7.5

Brachial valve moderately to deeply concave, least concave in visceral disc, sloping steeply to antero-lateral margins, some specimens geniculate; cardinal extremities moderately large in some specimens, well defined by strongly convex flexures; low fold formed on trail; ornamentation complementary to that of opposite valve but lacking spines; median costa represented by strong median furrow and elongate spine ridges are represented by elongate dimples; small protegulal node present medially at hingeline; cardinal process sessile, small, bilobed internally, supported by very stout median septum that extends forward over much of visceral disc; endospines coarse, radially arranged; other internal details not observed.

Distinguishing characters.—This species can be differentiated by its strongly inflated pedicle valve, evenly convex semicircular lateral profile, moderate fold and sulcus with medial ventral costa and dorsal medial furrow, rugose ventral visceral disc with elongated spine ridges, costate trails, scattered finer spines on the flanks, ears, and hingeline, and several coarse spines on the median costa of the pedicle valve.

Remarks.—*Mesoplica? mesicostalis* (Weller) is not similar to other North American Mississippian leioproductids. It bears some resemblance in shape and outline to several Devonian species belonging to this family but can be differentiated from them by its costate ornamentation. *Mesoplica praelonga* (J. de C. Sowerby), the type species of the genus from the Famennian of England, differs in being larger, in having a weaker sulcus, and in having weaker, more indistinct costae which extend onto the visceral disc. *Mesoplica praelonga simplicior* (Whidborne) from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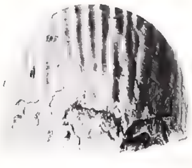
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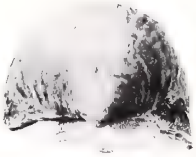
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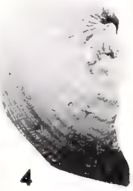
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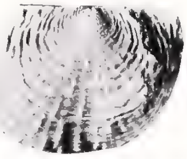
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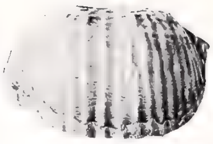
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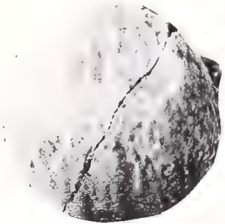
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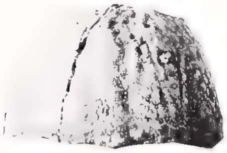
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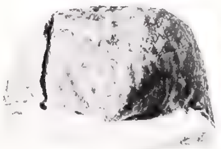
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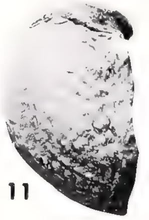
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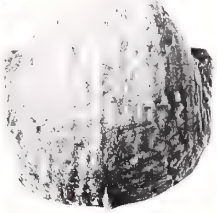
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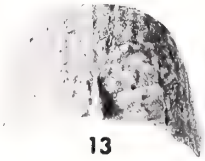
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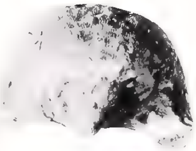
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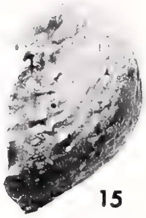
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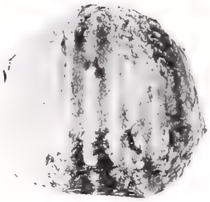
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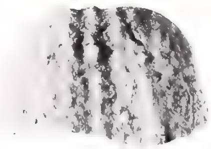
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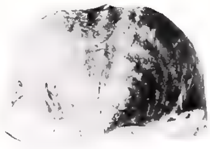
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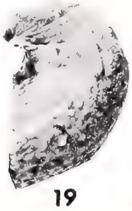
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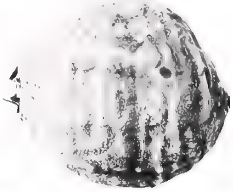
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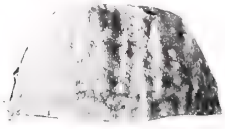
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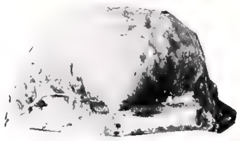
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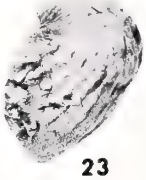
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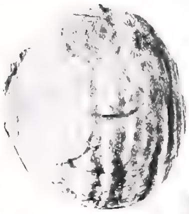
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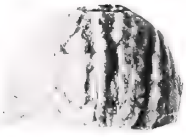
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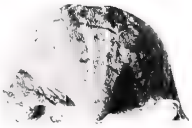
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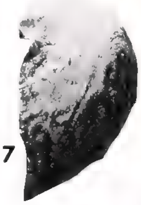
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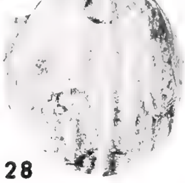
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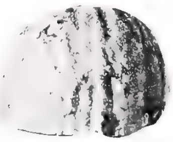
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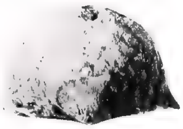
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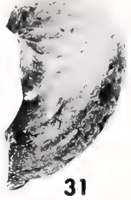
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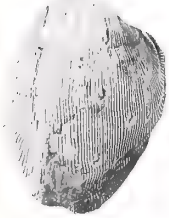
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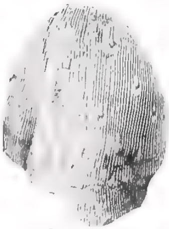
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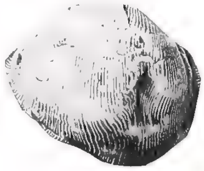
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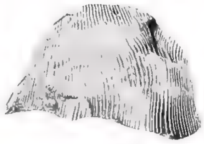
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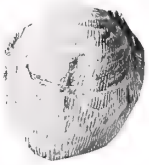
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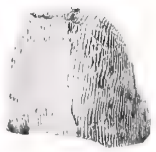
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the Famennian of England lacks a ventral sulcus, the median costa is weak or absent, and the costae extend onto the visceral disc. *Mesoplica praelonga semisbugensis* (Nalivkin) from the Famennian of Kazakhstan is larger than *Mesoplica? mesicostalis* (Weller), has very coarse costae, and a strong medial costa in the sulcus.

Distribution.—Weller described this species from the English River Sandstone of Washington County, Iowa. His collection of syntypes comprises only seven specimens, all indifferently preserved in soft sandstone. Van Tuyl (1925:56) reported this species in the English River Sandstone at Burlington, Des Moines County, Iowa.

In the Glen Park Formation *Mesoplica? mesicostalis* (Weller) occurs only at locality SL393, Pike County, Illinois (30 specimens).

Genus **Nigeroplica** Nalivkin, 1975

Nigeroplica? illinoisensis, new species

Fig. 7.1–7.31

Holotype.—Fig. 7.16–7.19, CM 34656, locality SL392, collected by the author, April 1985.

Paratypes.—Fig. 7.1–7.15, 7.20–7.31, CM 34652–34659, same collection as the holotype.

Description.—Medium size for genus, strongly concavo-convex, length and width subequal or more often longer than wide; greatest width attained anteriorly on trail or, more rarely, at hingeline; outline variable from longitudinally to transversely subovate to subquadrate; lateral profile semicircular to subguttate; auriculations small, well defined, subangular, compressed; both valves geniculate; trail moderately long in most specimens; body cavity thick; shell substance thin.

Pedicle valve strongly inflated, most convex in umbonal region and at point of geniculation; visceral disc more moderately convex; flanks sloping steeply to antero-lateral margins, trail weakly convex to almost straight in profile; venter variable in convexity from evenly convex to flattened or sulcate; sulcus weakly developed or lacking; anterior profile often subquadrate; umbo broad, beak small, slightly overhanging hingeline; ornament consisting of weak rugae and faint elongate spine ridges on posterior portion of visceral disc, ridges forming irregular costae anteriorly on visceral disc and trail; large median costa often present but absent in some specimens; lateral costae of variable strength and uniformity, sometimes merging, bifurcating or becoming obsolete on trail; suberect moderate diameter spines numerous over most of shell, often on crests of costae, being especially dense on lateral extremities, those near hingeline being slightly finer; several large diameter erect spines on median costa, when present; growth lines fine, sinuous; internal details not observed.

Table 14.—*Measurements (in mm) of the types of* Nigeroplica? illinoisensis, *new species.*

Specimen no.	Locality	Length	Width	Height	Surface measure
		Pedicle valves			
CM 34652	SL392	18.2	17.8	12.1	35.0
CM 34654	SL392	19.8	19.9	12.5	36.5
CM 34655	SL392	19.7	19.3	13.2	36.2
CM 34656	SL392	17.9	18.7	12.0	34.5
CM 34657	SL392	18.0	19.3	11.0	31.9
CM 34658	SL392	19.0	16.7	10.7	35.6
CM 34659	SL392	18.3	15.8	10.8	34.1
		Brachial valve			
CM 34653	SL392	15.6	19.1	7.8	—

Brachial valve strongly geniculated with weakly concave visceral disc, being strongly concave at point of geniculation, moderately concave on trail; trail moderately long; ears set off by weakly convex flexures; tiny protegulal node present at posteromedial margin; ornament consisting of rugae and elongate dimples on entire visceral disc and costae on trail; spines not observed; deep wide median intercostal furrow present on trail of most specimens; cardinal process small, sessile, bilobed internally, with small alveolus, supported by long median septum that extends forward almost to point of geniculation; other internal details not observed.

Distinguishing characters.—*Nigeroplica? illinoisensis* n. sp. can be recognized by its small size, geniculate valves, subquadrate anterior profile, ornamentation of rugae and spine ridges on the ventral visceral disc with costae on the trail, large median costa on most specimens, and numerous medium-sized erect spines over much of the pedicle valve, several large erect spines on the median costa, and with a deep, wide medial intercostal furrow on the trail of the brachial valve in many specimens.

Remarks.—Assignment of this species to the genus *Nigeroplica* Nalivkin, 1975, is based almost entirely on external morphology and ornamentation and comparison is made mainly with Soviet illustrations of the type species. The interior of the type species of this genus, *Productus niger* Gosselet, 1888, is not well known, nor is that of the present species from the Glen Park. Nalivkin (1975:160) originally

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Fig. 7.—Productids. 7.1–7.31, *Nigeroplica? illinoisensis* n. sp.; 7.1–7.7, small pedicle valve and small natural mold of brachial valve exterior with very well preserved ornament, CM 34652, 34653; 7.8–7.31, six pedicle valves, including the holotype (7.16–7.19), CM 34654–34659, all from SL392; all ×1.5. 7.32–7.37, *Ovatia nascens* n. sp.; 7.32, 7.33, ventral and anterior views of a pedicle valve, the holotype, CM 34660; 7.34–7.37, ventral and anterior views of two natural molds of brachial valve exteriors, CM 34661, 34662, all from SL392, all ×1.

assigned his new genus to the Family Avoniidae Sarycheva, 1960, but stated that it was one of the last representatives of the group of *Mesoplica praelonga* (J. de C. Sowerby). Later (1979:46), he reassigned it to the Family Leioproductidae Muir-Wood and Cooper, 1960, reaffirmed its similarity to *Mesoplica,* and compared it with the leioproductid genus *Argentiproductus* Cooper and Muir-Wood, 1951, and the overtoniid genus *Avonia* Thomas, 1914. These genera are not related and have radically different dorsal interiors. It is possible that *Nigeroplica* is a junior subjective synonym of the genus *Spinocarinifera* Roberts, 1971.

In North America, *Nigeroplica? illinoisensis* n. sp. is most similar to *Productus missouriensis* Branson, 1938, which may prove to be assignable to the genus *Nigeroplica.* Branson (1938*a*:163–164) based his species on six specimens from the "Bushberg Sandstone" of Montgomery County, Missouri. These specimens are all much larger than *Nigeroplica? illinoisensis* n. sp. and five of the six specimens are strongly transverse with a definite fold-sulcus, a rare occurrence in *Nigeroplica? illinoisensis* n. sp. In addition, the "Bushberg" species seems to lack the large medial costa with strong erect spines that characterize the Glen Park form.

Spinocarinifera copiosa Carter, 1987, from the Banff Formation of Alberta, is similar to *Nigeroplica? illinoisensis* n. sp. in its size, outline, profile, and ornamentation, excluding spine distribution. It differs in having a much longer trail, a flattened venter in many specimens, a much narrower hingeline, and a dense brush of spines on the lateral extremities.

Nigeroplica niger (Gosselet), the type species, from the late Famennian and early Tournaisian of Eurasia, differs from *Nigeroplica? illinoisensis* n. sp. in having an evenly convex non-geniculate lateral profile, and the common development of a flattened venter or sulcus. A strong median costa with coarse erect spines is not developed in specimens from Belgium.

Productus (Avonia) schindewolfi Paeckelmann, 1931, from the Late Famennian or Early Tournaisian of Germany is similar to *Nigeroplica? illinoisensis* n. sp. in outline and geniculate lateral profile, and in the possession of a strong median costa with several strong erect coarse spines. It differs in having smaller auriculations, weaker ribbing on the flanks, and a more convex rounded anterior profile.

Distribution.—Nigeroplica? illinoisensis n. sp. has been found only at locality SL392, Pike County, Illinois (44 specimens).

Subfamily Productininae Muir-Wood and Cooper

Genus *Argentiproductus* Cooper and Muir-Wood, 1951

Argentiproductus auriculatus, new species

Fig. 6.33–6.50

Holotype.—A pedicle valve, Fig. 6.33–6.36, CM 34649, collected by the author at SL393, 1985.

Paratypes.—A pedicle valve, Fig. 6.37–6.40, IGS 80P34, collected by C. Collinson; two pedicle valves, CM 34650, 34651, Fig. 6.41–6.48, collected by the author in 1985; a brachial valve exterior, Fig. 6.49, IGS 80P35, collected by C. Collinson; an imperfect brachial valve interior, IGS 80P36, collected by C. Collinson; all from SL393.

Description.—Small for the genus, moderately concavo-convex, much wider than long, greatest width attained at or near hingeline; outline tranversely subelliptical; body cavity thin.

Pedicle valve moderately inflated with broad umbonal region most strongly convex and projecting notably beyond hingeline; lateral profile subguttate to semicircular, slightly geniculate in large specimens; anterior profile slightly arched medially with gently convex flanks sloping gradually to antero-lateral margins; cardinal extremities extended into moderately large, slightly compressed auriculations well delimited by concave flexures; beak moderately large, incurved over hingeline; ornamentation consisting of squamous growth lamellae and four to six, coarse to medium, mostly simple, rounded costellae per 3 mm at the anterior margin, which infrequently increase by bifurcation; intercostal furrows narrow; spine bases erect or suberect and coarse for size of specimens, rare on venter and flanks, with one pair on sides of umbo, and two pairs on auriculations; interior with moderately impressed ventral muscle field and strongly developed ear baffles that are not externally apparent.

Brachial valve moderately to deeply concave, with short trail; small protegulal node present at hingeline; cardinal extremities delimited by slightly convex flexures; ornamentation consisting only of regularly lamellose growth lamellae in small specimens, exterior of large specimens not observed; interior with small sessile trilobed cardinal process; lateral ridges diverging moderately from hingeline, not reaching auriculations; length of median septum not observed; endospines numerous, becoming coarse anteriorly; trail much thickened with secondary shell tissue, with depressed medial sulcus bordered by rows of strong endospines; brachial ridges and other internal details not observed.

Distinguishing characters.—Argentiproductus auriculatus n. sp. is characterized by its small size, tranverse outline, large auriculations, medium to coarse costellae, ear baffles in the pedicle valve, and much thickened dorsal trail.

Remarks.—Argentiproductus auriculatus n. sp. is not similar to other North American productinines, being much more transverse and lower in profile than such common species as *Productina sampsoni* (Weller) or *Productina parvula* (Winchell). *Productina lodgepolensis* Rodriguez and Gutschick, from the Lodgepole Limestone of Montana, is similar in being transverse with the greatest width at the hingeline and in having a low profile, but differs in being proportionately narrower, having much smaller auriculations, and much finer ribbing.

Argentiproductus margaritacea (Phillips), the type species from the Viséan of northern Europe and Australia, differs from *Argentiproductus auriculatus* n. sp. in being much larger with relatively smaller auriculations. *Argentiproductus rjausakensis* Nalivkin, from the late Famennian of the southern Urals, is very similar in outline and costation to *Argentiproductus auriculatus* n. sp. but differs in being somewhat larger with more acutely triangular auriculations. Spine patterns and the presence or absence of ear baffles in the pedicle valve are not known for the Soviet species.

Distribution.—This description is based on single collections of 24 specimens, all from locality SL393, Brown Branch, Pike County, Illinois.

Family Overtoniidae Muir-Wood and Cooper
Subfamily Sentosiinae Nalivkin
Genus *Sentosia* Muir-Wood and Cooper, 1960

Sentosia? ignota**, new species**
Fig. 8.1–8.17

Holotype.—A pedicle valve, Fig. 8.7–8.10, CM 34665, collected by the author from SL393.

Paratypes.—Pedicle valve, Fig. 8.1, CM 34663, same collection as the holotype; pedicle valve, Fig. 2, IGS 80P37, collected by C. Collinson; pedicle valve, Fig. 8.3–8.6, CM 34664, same collection as the holotype; pedicle valve, Fig. 8.11–8.14, IGS 80P38, collected by C. Collinson; natural mold of brachial valve exterior with cardinal process preserved at hingeline, Fig. 8.15, CM 34666, same collection as the holotype; natural mold of brachial valve exterior with cardinal process preserved, Fig. 8.16, IGS 80P39, collected by C. Collinson; small natural mold of brachial valve exterior, Fig. 8.17, IGS 80P40, collected by C. Collinson. All specimens are from Brown Branch, Pike County, Illinois, locality SL393.

Description.—Medium size for genus, moderately concavo-convex, transversely subelliptical in outline, wider than long; maximum width attained near midlength; fold and sulcus lacking; lateral profile low, semilenticular to semichordate; auriculations moderately developed, well rounded, delimited by concave flexures; trail short, body cavity thin.

Pedicle valve moderately inflated, most convex in umbonal region, evenly convex on venter, weakly convex on flanks, ears moderately compressed; anterior profile semiprolate; umbonal region moderately inflated, posteriorly produced, overhanging hingeline; beak small, incurved; ornament consisting of numerous closely spaced, elongate spine ridges, arranged in quincunx, sometimes coalescing to form irregular costellae on venter, especially anteriorly; weak irregular rugae present, mostly on umbonal region; growth lines very fine, regularly spaced, sinuous; spine bases round and relatively coarse, that is, almost as thick as spine ridges, present on each spine ridge and distributed almost evenly over entire valve surface; inclination of spines not determinable; interior with numerous densely spaced endospines and moderately impressed muscle field.

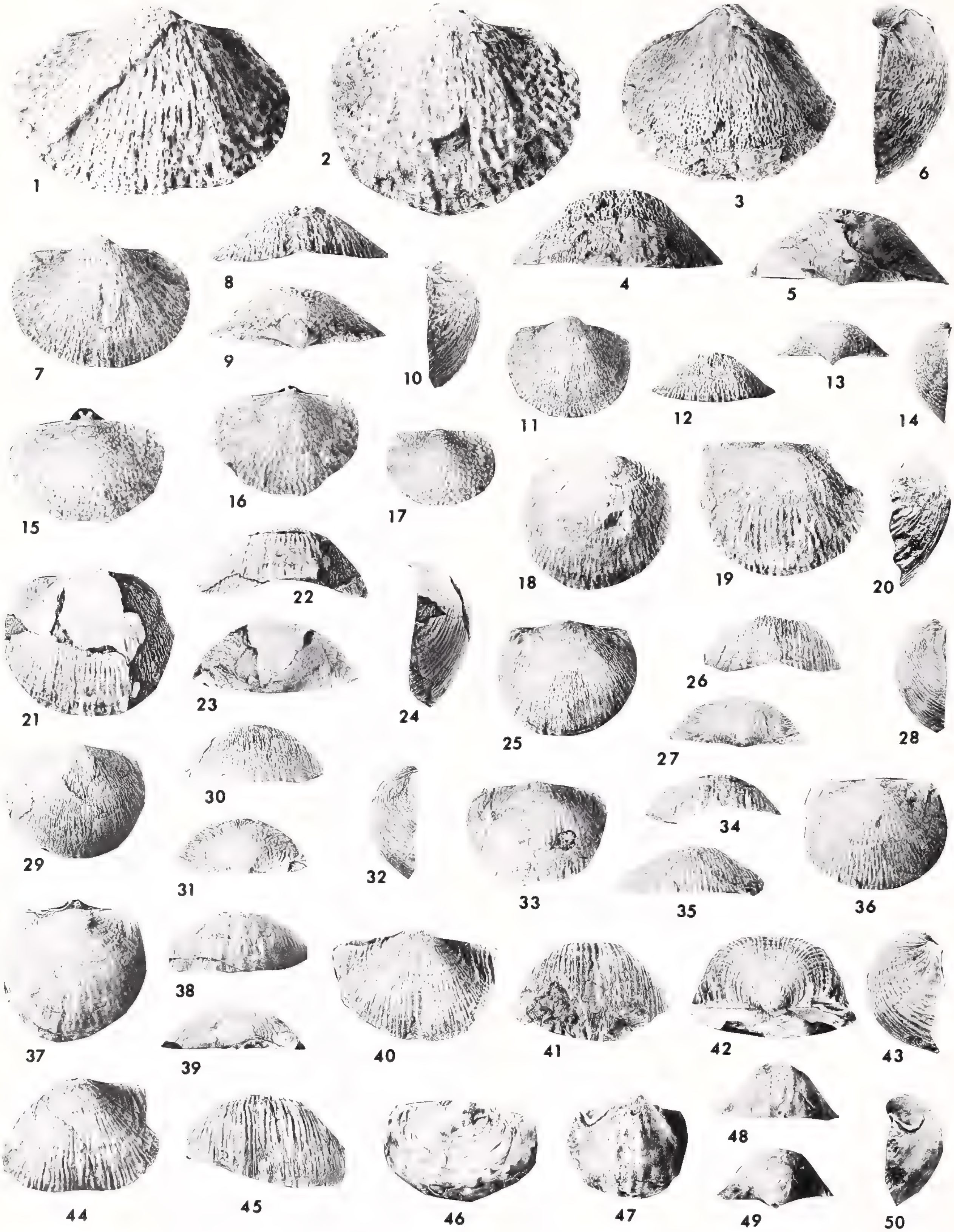
Brachial valve moderately and evenly concave except for postero-medial depression and cardinal extremities which are defined by low, slightly convex flexures; ornament consisting of slightly elongate dimples arranged in quincunx, very weak irregular rugae, and fine regularly spaced sinuous growth lines; spine bases very fine, sparsely scattered; interior with small sessile bilobed cardinal process; lateral ridges short, diverging slightly from hingeline; endospines very long and fine anteriorly, densely arranged on trail; other internal details not observed.

Table 15.—*Measurements (in mm) of the types of* Argentiproductus auriculatus, *new species, all from locality SL393.*

Specimen no.	Length	Width	Height	Surface measure
		Pedicle valves		
CM 34649	9.8	13.7	5.3	16.0
IGS 80P34	9.3	11.8	4.6	14.3
CM 34650	8.0	11.2	4.3	11.3
CM 34651	7.6	9.5	3.5	11.0
		Brachial valves		
IGS 80P35	3.2	5.0	—	—
IGS 80P36	8.0	10.4	3.1	—

Distinguishing characters.—This species is characterized by its transversely subelliptical outline, moderately arched venter with flattened or weakly convex flanks, and ornamentation of elongate spine ridges arranged in quincunx that tend to coalesce anteriorly on the pedicle valve and slightly elongate dimples arranged in quincunx on the brachial valve.

Remarks.—*Sentosia? ignota* n. sp. is not similar to other North American productids. Its unusual ornamentation of elongated spine ridges arranged in quincunx over the whole pedicle valve and tending to coalesce into irregular costae is reminiscent of the genus *Rhytiophora* Muir-Wood and Cooper, 1960. The latter genus, however, is much more convex with a much broader umbo, has coarser ornamentation with strongly rugose valves, and well developed angular auriculations. Assignment of this species to the genus *Sentosia* Muir-Wood and Cooper is speculative and based upon similarity in shape, outline, degree of inflation, and general pattern of ornamentation. This new Glen Park species differs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from the Famennian type species, *Sentosia praesursor* (Stainbrook), in having much coarser ornamentation. Furthermore, the type species has a flattened venter and much less arched anterior profile. The interior of the Glen Park species is poorly known. For these reasons, assignment of this new species to the genus *Sentosia* is not certain.

Sentosia kysarkensis Nalivkin, 1979, from the Famennian of the southern Urals bears some similarity to *Sentosia? ignota* n. sp. in its ornamentation on both valves, but the Soviet species appears to be much more elongated with subangular auriculations. *Productus* (*Waagenoconcha*) *nurensis* Nalivkin, as described and illustrated by Litvinovich et al. (1975), from the Lower Tournaisian of Kazakhstan, is similar to *Sentosia*? *ignota* n. sp. in outline and general type of ornamentation but differs in being much larger with weaker ribbing on the ventral trail.

Distribution.—This description is based on a single collection of 15 specimens from locality SL393, Brown Branch, Pike County, Illinois.

Subfamily Overtoniinae Muir-Wood and Cooper

Genus ***Avonia*** Thomas, 1914

Avonia sp.

Fig. 8.47–8.50

Referred specimen.—A small spalled pedicle valve, IGS 80P47, collected by C. Collinson from SL393, Brown Branch, Pike County, Illinois.

Description.—This description is based on a single pedicle valve. Smaller than average for genus, strongly convex, slightly wider than long, outline transversely subovate; maximum width attained anterior to hingeline near midlength; lateral profile semichordate to subguttate; ears moderately large, well defined, compressed; umbonal region inflated, moderately narrow, extending well posterior to hingeline; beak small, narrow, overhanging hingeline; venter arched with almost triangular anterior profile; flanks weakly convex, sloping steeply to lateral margins; trail short; ornament poorly preserved due to spalling of surficial shell layers but consisting of at least several relatively coarse simple rounded costellae on venter; spine bases poorly preserved but at least one pair of relatively coarse erect spine bases present on sides of umbo; other details not observed.

Table 16.—*Measurements (in mm) of the types of* Sentosia? ignota, *new species, all from locality SL393.*

Specimen no.	Length	Width	Height	Surface measure
		Pedicle valves		
CM 34663	11.6	16.7	6.0	16.0
IGS 80P37	12.6	15.5	4.8	16.7
CM 35664	21.4	+25.7	10.0	31.2
CM 34665	15.8	21.5	7.4	22.4
IGS 80P38	12.1	14.9	5.8	16.4
		Brachial valves		
CM 34666	13.5	18.6	3.6	—
IGS 80P39	13.1	18.2	3.6	—
IGS 80P40	9.2	13.1	2.9	—

Measurements (in mm).—Length, 6.5; width, 7.3; height, 3.6; surface measure, 9.3.

Remarks.—This unique specimen is quite different from any other productid in the Glen Park Formation by virtue of its narrow inflated umbo and weakly costellate ornament. Assignment to the common Lower Carboniferous genus *Avonia* Thomas is based on its small size, subovate outline, arched venter, inflated narrow umbo with an incurved beak, and weakly costellate ornamentation. The writer is unaware of any comparable species in North America.

Genus ***Semiproductus*** Bublichenko, 1956

Semiproductus sp.

Fig. 8.40–8.45

Referred specimens.—Two pedicle valves, IGS 80P45, 80P46, collected by C. Collinson from Brown Branch, Pike County, Illinois, locality SL393.

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Fig. 8.—Productids. 8.1–8.17, *Sentosia? ignota* n. sp.; 8.1, 8.2, two small pedicle valves showing spine base distribution, CM 34663 and IGS 80P37, respectively; 8.3–8.14, ventral, anterior, posterior and lateral views of three pedicle valves, including the holotype (8.7–8.10), CM 34664, 34665 and IGS 80P38, respectively; 8.15, 8.16, two spalled brachial valve interiors with cardinal process preserved, CM 34666 and IGS 80P39, respectively; 8.17, natural mold of brachial valve exterior, IGS 80P40, all from SL393; all × 1.5 except 8.1 and 8.2, × 3. 8.18–8.39, *Whidbornella curtirostris* (Winchell); 8.18, the lectotype, UMI 1337, a pedicle valve from the English River Sandstone at Burlington, Iowa; 8.19, 8.20, ventral and lateral views of the natural mold of a brachial valve, a paralectotype, UMI 1337, same locality as the lectotype, both from White Collection; 8.21–8.35, ventral, anterior, posterior and lateral views of four pedicle valves, IGS 80P41–80P43, CM 34667, respectively; 8.36, natural mold of a brachial valve exterior, CM 34668; 8.37–8.39, spalled brachial valve interior showing cardinal process, IGS 80P44, 8.21–8.39 all from SL393; all × 1. 8.40–8.45, *Semiproductus* sp.; 8.40–8.43, ventral, anterior, posterior and lateral views of a nearly complete pedicle valve, IGS 80P45; 8.44, 8.45, ventral and anterior views of an incomplete pedicle valve, IGS 80P46; both from SL393; × 1. 8.46, *Quadratia?* sp., a spalled brachial valve exterior from SL397, CM 34669, × 1. 8.47–8.50, *Avonia* sp., ventral, anterior, posterior and lateral views of a pedicle valve from SL393, IGS 80P47, × 3.

Table 17.—*Measurements (in mm) of referred specimens of* Semiproductus *sp. from locality SL393.*

Specimen no.	Length	Width	Height	Surface measure
IGS 80P45	22.6	30.3	13.7	39.0
IGS 80P46	22.3	+30.0	15.1	+36.0

Description.—Average size for genus, strongly convex, much wider than long, outline transversely subquadrate; greatest width attained at hingeline; auriculations moderately large, compressed, subangular; umbo broad, not inflated, moderately produced posteriorly; beak small, slightly overhanging hingeline; visceral disc flattened, moderately convex; lateral profile geniculate; anterior profile subtrapezoidal; venter of visceral disc flattened, trail with shallow but distinct sulcus on both specimens; flanks sloping steeply to lateral margins; trail short but specimens may be incomplete; reticulate ornamentation consisting of numerous moderately coarse rugae and weak spine ridges in umbonal region, rugae and costae on remainder of visceral disc; well developed costae present on trail; costae numbering about 10 or 11 per cm at anterior margin; spine bases rare on trail and flanks, usually with two strong bases on costa in center of sulcus; spine bases more numerous near hingeline and sides of umbo, not seemingly arranged in any consistent pattern; brachial valve, depth of body cavity, and interiors unknown.

Remarks.—Authentic large reticulate productids are unreported in the late Famennian and earliest Mississippian of North America. Assignment of these pedicle valves to the Soviet genus *Semiproductus* Bublichenko is based solely on external morphological characters. The Glen Park specimens differ from pedicle valves of the type species, *Semiproductus minax* Bublichenko, 1956, mainly in having stronger radial ornamentation. In this respect, the Glen Park specimens most closely resemble *Semiproductus speluncus* Nalivkin, 1979, from the late Famennian of the southern Urals. The latter can be readily differentiated from the Glen Park species by its much larger size, broader sulcus and much coarser ornamentation.

Family Linoproductidae Stehli
Subfamily Linoproductinae Stehli
Genus **Ovatia** Muir-Wood and Cooper, 1960

Ovatia nascens, new species
Fig. 7.32–7.37

.1914 *Productus ovatus* Hall: Weller, pl. 16, fig. 13; not fig. 1–12, 14, 15.

Holotype.—A pedicle valve, Fig. 7.32–7.33, CM 34660, collected by the author from SL392, May 1984.

Paratypes.—Two natural molds of brachial valve exteriors, Fig. 7.34–7.37, CM 34661, 34662, same collection as the holotype.

Description.—Average size for genus, strongly gibbous, longer than wide with maximum width attained near midlength; outline subovate; ears small, subangular, well defined by concave flexures, much compressed; brachial valve slightly geniculated; body cavity thin.

Pedicle valve strongly convex, most convex in umbonal region, becoming much less convex anteriorly; narrow gibbous umbonal region extending posterior to hingeline; beak narrow, incurved, overhanging hingeline; flanks sloping steeply to lateral margins; venter evenly rounded, anterior profile almost U-shaped; trail moderately long, usually flaring moderately; entire surface costellate with about 25–27 costellae per cm as measured 25 mm from ventral beak (surface measure); costellae increase by intercalation except by bifurcation anterior to spine bases; six or seven strong rounded rugae present on each side of umbonal region and on ears but not extending around umbo; growth lines very fine, closely spaced, irregular in strength; fine spine bases sparsely and almost evenly scattered on crests of costellae over entire surface of valve; hinge spine bases not observed; internal details not observed.

Brachial valve geniculate with moderately concave visceral disc; trail less concave, at about right angle to visceral disc in two paratypes; ears well delimited by convex flexures; trail evenly concave on dorsum, sloping steeply to lateral margins, forming U-shaped anterior profile as in opposite valve; ornamentation similar to that of pedicle valve but with very weak rugae across visceral disc; fewer and smaller spine bases than on pedicle valve; internal details not observed.

Distinguishing characters.—*Ovatia nascens* n. sp. can be differentiated by its ornament of 25–27 costellae per cm at a surface measurement of 25 mm from the ventral beak, by its thin body cavity, and the very weak rugae on the visceral disc of the brachial valve.

Remarks.—This new species is similar to two other Lower Mississippian species of the genus *Ovatia* Muir-Wood and Cooper. They are *Ovatia laevicosta* (White), from the Wassonville Dolomite of southeastern Iowa, and *Ovatia prolata* Carter, 1987, from the Banff Formation of Alberta. *Ovatia laevicosta* differs from this new Glen Park species in having a less inflated, broader, umbonal region and coarser costellae, about 20–27 per cm measured at a surface measure distance of 25 mm from the ventral beak. *Ovatia prolata* has finer costellae than *Ovatia nascens* n. sp., about 30–40 per cm at a surface measure distance of 25 mm from the ventral beak, has much stronger rugae on the visceral disc of the brachial valve, and has fewer rugae on the sides of the umbonal region.

Weller (1914:pl. 16, fig. 13) figured a specimen of this species from the English River Sandstone at Burlington, Iowa, as *Productus ovatus* Hall, 1858.

Table 18.—*Measurements (in mm) of types of* Ovatia nascens *n. sp. from locality SL392.*

Specimen no.	Length	Width	Height	Surface measure
Holotype (PV)				
CM 34660	33.9	+22.3	16.1	51.9
Paratype (BV)				
CM 34661	25.2	−27.9	15.2	41.4
Paratype (BV)				
CM 34662	23.9	20.4	15.6	37.7

Although this species marks the lowest occurrence of the genus *Ovatia* in North America, it is probable that the genus occurs in Famennian age beds in the Soviet Union. It has been reported in late Famennian (or Etroeungt) age beds of Kazakhstan by Grechishnikova (1966), Bublichenko (1971) and Litvinovich et al. (1975), from the late Famennian of the southern Urals by Nalivkin (1979), and from Famennian age beds in Timan-Pechora by Fotieva (1985).

Distribution.—This description is based on a collection of 11 specimens from Horton Creek, Pike County, Illinois, SL392. One other pedicle valve was recovered from locality SL393. This species is moderately common in the English River Sandstone in the vicinity of Burlington, Iowa. Although these English River specimens are preserved in a soft coarse sandstone, they agree in all determinable morphological characters with the Glen Park specimens from Pike County, Illinois.

Order Pentamerida Schuchert and Cooper
Suborder Syntrophiidina Ulrich and Cooper
Superfamily Stenoscismatacea Oehlert
Family Atriboniidae Grant
Subfamily Atriboniinae Grant
Genus ***Sedenticellula*** Cooper, 1942

Sedenticellula hamburgensis (Weller, 1910)

Fig. 9.17–9.45, 10

*1910 *Camarophoria hamburgensis* Weller: p. 500–501, fig. 2.
v*1914 *Camarophoria hamburgensis* Weller: Weller, p. 170–172, pl. 23, fig. 52–60; text-fig. 2.
1965*a* *Sedenticellula hamburgensis* (Weller): Grant, p. 73–75, pl. 21, fig. 1–12; text-fig. 14.
1965*b* *Sedenticellula hamburgensis* (Weller): Grant, *in* Williams et al., fig. 511: 1a–c; 512: 1a–o.

Lectotype.—Designated by Grant, 1965*a*, as FMNH UC13937, illustrated by Weller, 1914, pl. 23, fig. 57; illustrated here as Fig. 9.17.

Table 19.—*Measurements (in mm) of the illustrated specimens of* Sedenticellula hamburgensis *(Weller), including the lectotype.*

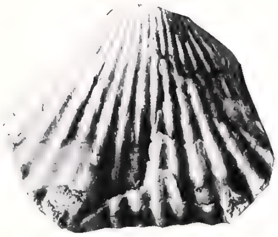
Specimen no.	Locality	Length	Width	Thickness
Lectotype (brachial valve)				
FMNH UC13937	SL395	10.7	13.3	4.3
Referred specimens				
CM 34671	SL392	12.5	13.9	7.1
CM 34673	SL397	11.3	12.2	6.6
CM 34672	SL392	10.2	10.8	5.8
IGS 80P48	SL392	9.6	11.1	5.7
IGS 80P49	SL392	8.3	8.4	4.2
IGS 80P50	SL392	6.8	6.1	2.6
IGS 80P51	SL392	5.4	5.2	2.4

Diagnosis.—Small for the genus, distinctly rostrate, outline subpentagonal to subtrigonal; ventral beak ridges angular and slightly compressed; brachial valve much more convex than pedicle valve in mature specimens; fold and sulcus well defined and of moderate breadth; ribs simple and subangular; ventral spondylium sessile posteriorly but rising slightly on a short septum anteriorly or with low septum obscured by callus.

Comparisons.—The only other species assigned to this genus is *Sedenticellula sacra* Grant, 1965, of Late Kinderhookian or Early Osagean age, from the Chappel Limestone of central Texas. This younger species differs greatly from the type species in its larger size, broad subelliptical outline, small ventral beak, broad fold and sulcus, and numerous bifurcating costae.

Remarks.—Weller (1910, 1914) mistakenly believed that the spondylium was completely sessile in this species. All specimens sectioned by this writer have clearly shown the presence of a low but distinct septum in the pedicle valve (see Fig. 10, sections 2.7 and 3.2). The septum shows clearly in thin section but is often obscured by shell callus, especially in longitudinal view, except at the anterior termination of the spondylium in mature specimens. Virtually all of the juvenile specimens observed have a distinct septum except near the beak where the spondylium is sessile in all specimens, both juvenile and adult.

Distribution.—This is one of the most common species in the oolitic facies of the Glen Park Formation, occurring in great numbers at localities SL393, SL395 and SL397. A single specimen was found at SL396. Weller (1906) failed to recover this species at Glen Park, Missouri (SL397) but this writ-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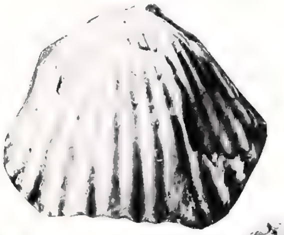
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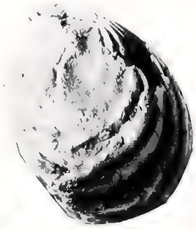
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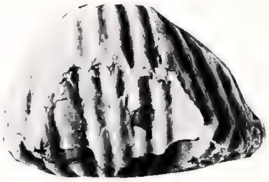
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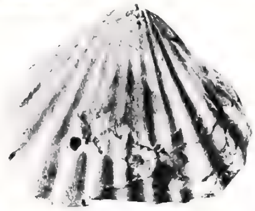
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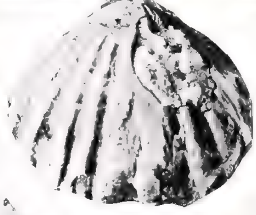
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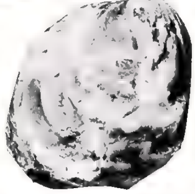
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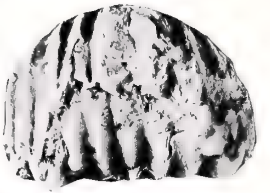
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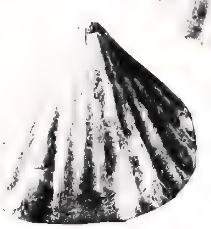
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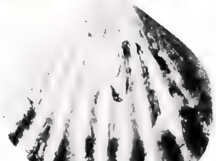
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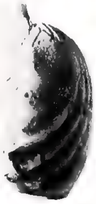
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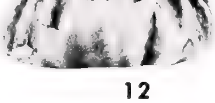
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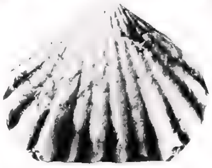
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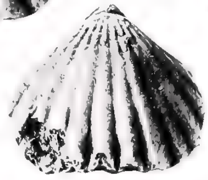
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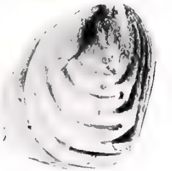
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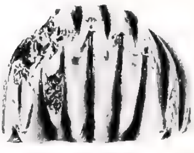
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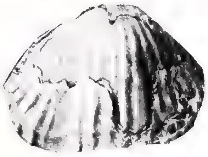
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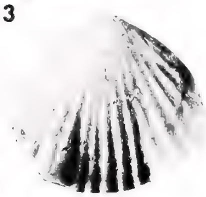
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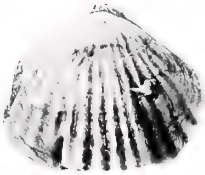
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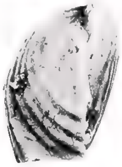
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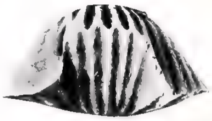
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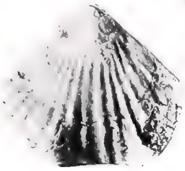
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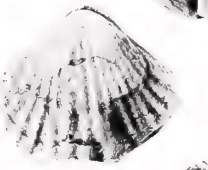
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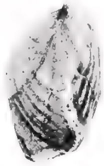
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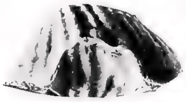
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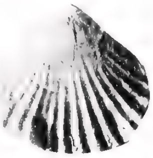
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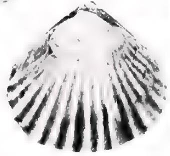
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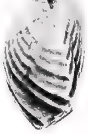
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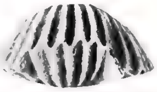
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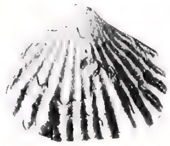
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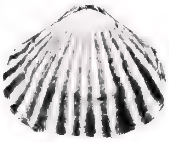
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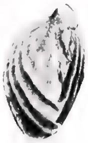
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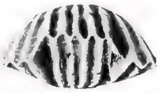
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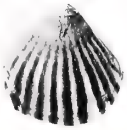
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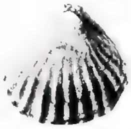
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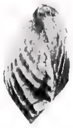
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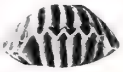
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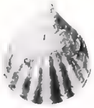
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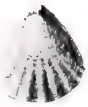
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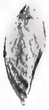
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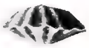
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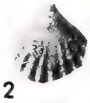
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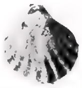
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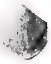
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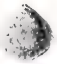
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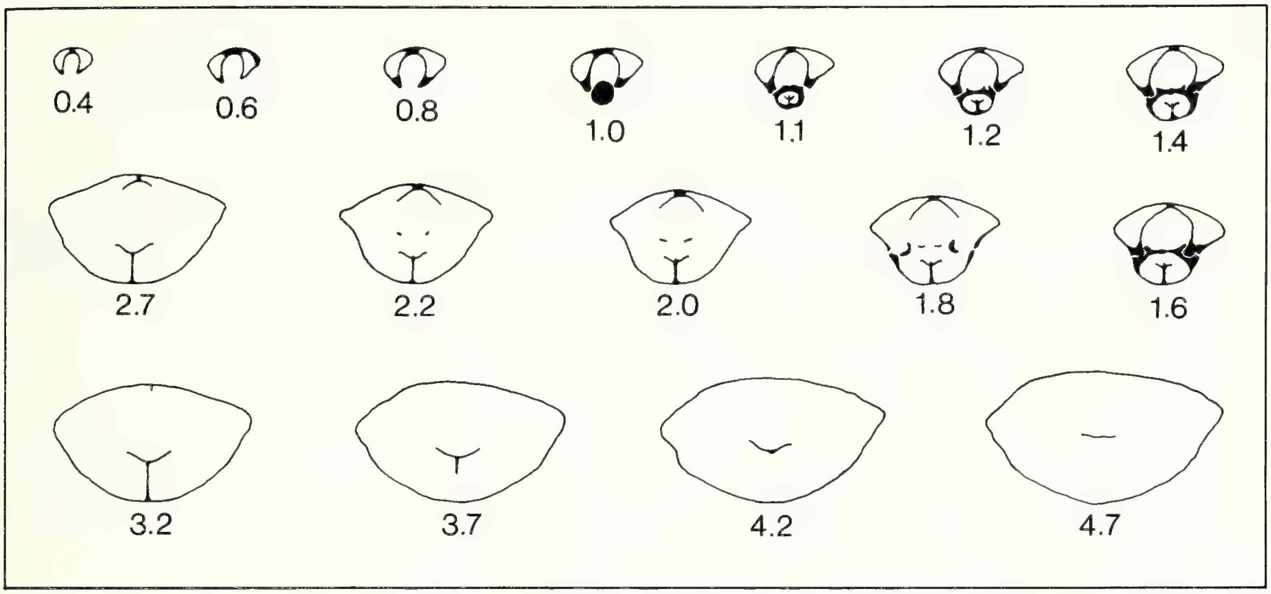

Fig. 10.—Transverse serial sections of *Sedenticellula hamburgensis* (Weller) from SL393, CM 34674. Numbers refer to distance in mm from ventral beak. ×3.

er found it to be one of the most common species there.

Order Rhynchonellida Kuhn
Superfamily Rhynchonellacea Gray
Family Pugnacidae Rzhonsnitskaya
Genus **Shumardella** Weller, 1910

Shumardella fracta, new species
Fig. 11.1–11.35, 12

Holotype.—CM 34675, Fig. 11.1–11.5, collected by the author from locality SL392, Horton Creek, Pike County, Illinois.

Paratypes.—CM 34676–34681, Fig. 11.6–11.35, same collection as the holotype.

Description.—Medium size for the genus, unequally biconvex, transversely subtrigonal in outline, greatest width attained anterior to midlength; lateral profile subtrigonal to subovate; anterior commissure strongly uniplicate, slightly serrate; fold and sulcus produced in anterior half of shell becoming broad and shallow near anterior margin with moderately large tongue; lateral margins slightly curved or straight but not serrate; cardinal margins slightly compressed; ribs poorly developed on both fold-sulcus and flanks; sulcus bald or with one to three weak subangular plicae; flanks bald or with one to three weak to moderately well expressed subangular plicae; growth varices irregularly spaced; moderately coarse irregular growth lines present but other micro-ornament, if any, not preserved.

Pedicle valve shallow except for tongue, gently convex posteriorly, sloping more steeply near lateral margins and in sulcus; umbonal region not inflated; beak small, short, slightly incurved, forming beak angle of 90 degrees or more; beak ridges moderately well defined, forming short palintropes on each side of beak; delthyrium obscured by dorsal umbo; deltidial plates not observed; sulcus originating in anterior half of valve, becoming broader but remaining shallow throughout, forming emarginate outline; plicae, if present, originating near margins in all specimens observed; interior with very short slender moderately diverging dental plates; teeth very small; muscle field not impressed.

Brachial valve much more inflated than opposite valve, becoming strongly inflated and tumid medially and sloping steeply to antero-lateral margins; maximum depth attained near anterior margin; umbonal region moderately convex, defined by short shallow concave lateral flexures; beak small, obscured by ventral valve in some specimens; fold not well defined, originating anterior to umbonal region; lateral plicae weaker and more obscure than those of opposite valve; interior with very short, open septalium supported by short low median septum which extends forward into posterior portion of umbonal region; outer hinge plates moderately depressed medially, attached to ventro-medial

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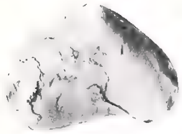
Fig. 9.—Rhynchoporids and pentamerids. 9.1–9.16, *Rhynchopora hamburgensis* Weller; 9.1–9.4, ventral, dorsal, lateral and anterior views of the lectotype, FMNH UC7742, from SL395; 9.5–9.12, ventral, dorsal, lateral and anterior views of two paralectotypes from SL395, FMNH UC7742; 9.13–9.16, ventral, dorsal, lateral and anterior views of a nearly complete specimen from SL392, CM 34670; all ×3. 9.17–9.45, *Sedenticellula hamburgensis* (Weller); 9.17, the lectotype, a brachial valve, FMNH UC13937; 9.18–9.45, ventral, dorsal, lateral and anterior views of seven specimens from SL393 (9.18–9.21, 9.26–9.45) and SL397 (9.22–9.25), CM 34671–34673, IGS 80P48–80P51, respectively; all ×2.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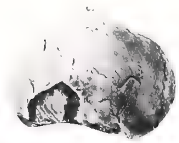
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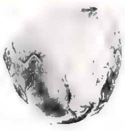
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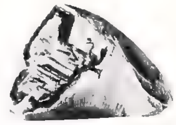
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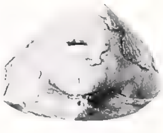
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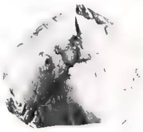
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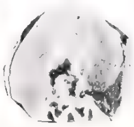
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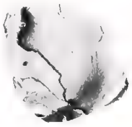
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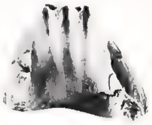
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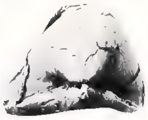
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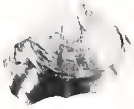
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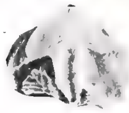
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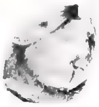
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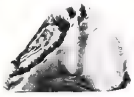
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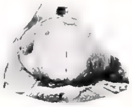
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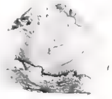
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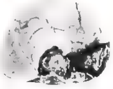
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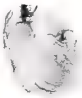
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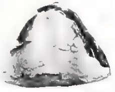
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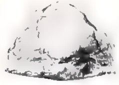
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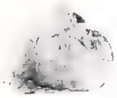
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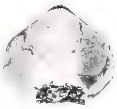
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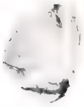
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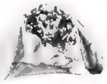
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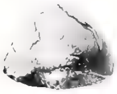
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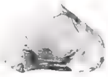
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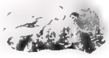
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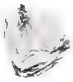
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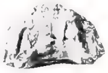
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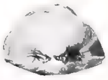
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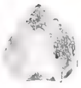
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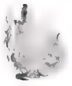
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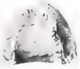
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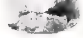
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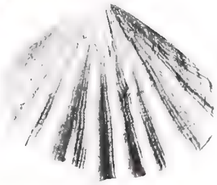
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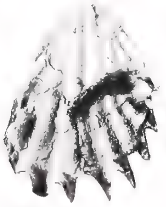
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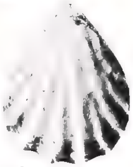
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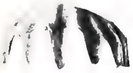
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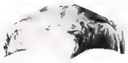
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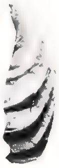
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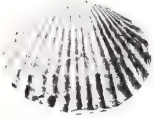
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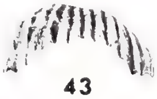
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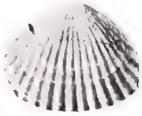
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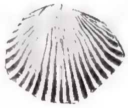
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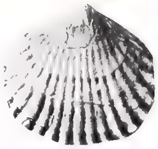
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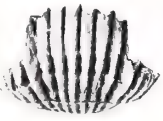
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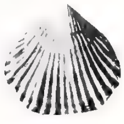
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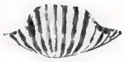
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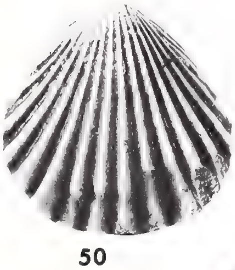
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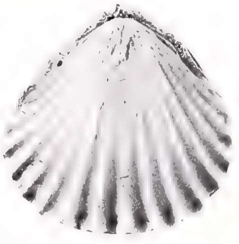
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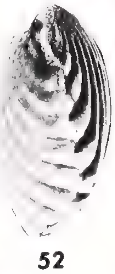
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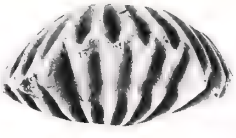
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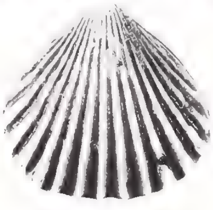
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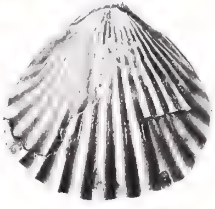
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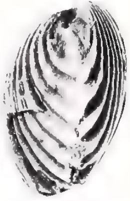
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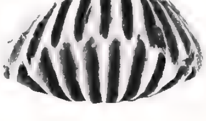
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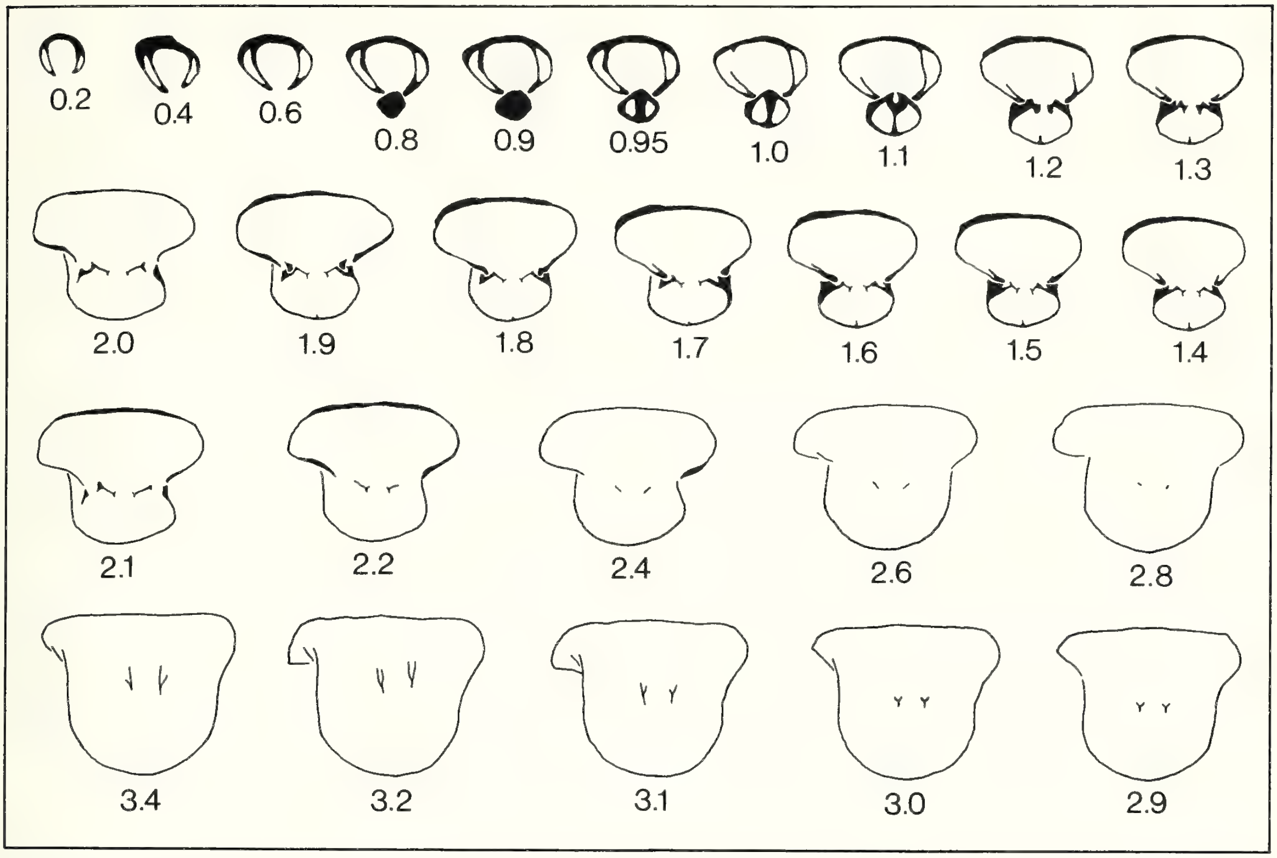

Fig. 12.—Transverse serial sections of *Shumardella fracta* n. sp. from SL392, CM 34686. Numbers refer to distance in mm from ventral beak. ×3.

edges of inner socket ridges; crural bases small, directed slightly laterally, slightly arcuate; crura short to moderate in length, broad and flat posteriorly, becoming very thin before becoming ventrally concave and curving ventrally, forming ventrally concave Y-shaped processes supported by low dorsally directed vertical plates; muscle field not observed in transverse section.

Distinguishing characters.—The weak ribbing on both fold-sulcus and flanks, subtrigonal outline with greatest width anterior to midlength, and broad shallow fold-sulcus serve to distinguish this species from similar related taxa.

Remarks.—This weakly ribbed species is most similar to the common Chouteau Limestone form *Shumardella obsolescens* Weller, 1910. It differs from the latter in its larger size, subtrigonal outline, broader fold-sulcus, and flatter pedicle valve. "*Leiorhynchus*" *greenianum* (Ulrich, 1886), from the Borden Group of Indiana, is another weakly ribbed species commonly assigned to the genus *Shumardella.* It differs from this new Glen Park species in being much larger with an extremely gibbous brachial valve and subovate outline.

Distribution.—This description is based on a single collection of 26 specimens from SL392, Horton

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Fig. 11.—Rhynchonellids. 11.1–11.35, *Shumardella fracta* n. sp.; ventral, dorsal, lateral, anterior and posterior views of a growth series of seven specimens from SL392 including the holotype (11.1–11.5), CM 34675–34681, ×1. 11.36, *Paraphorhynchus* sp., a small pedicle valve from SL393, CM 34682, ×2. 11.37–11.41, *Axiodeaneia glenparkensis* n. sp.; 11.37, a large pedicle valve from SL397, CM 34683; 11.38–11.41, dorsal, anterior, posterior and lateral views of a brachial valve from SL396, the holotype, CM 34684, all ×1. 11.42–11.49, *Rhynchopora prisca* n. sp.; 11.42, 11.43, dorsal and anterior views of a large brachial valve, CM 34685, the holotype, ×1; 11.44, 11.45, two smaller brachial valves, IGS 80P52, 80P53, ×1; 11.46–11.49, ventral and anterior views of two smaller pedicle valves, IGS 80P54, 80P55, ×1.5; all from SL393. 11.50–11.57, *Rhynchopora hamburgensis* Weller, ventral, dorsal, lateral and anterior views of two shells from SL511, IGS 80P56, 80P57, ×3.

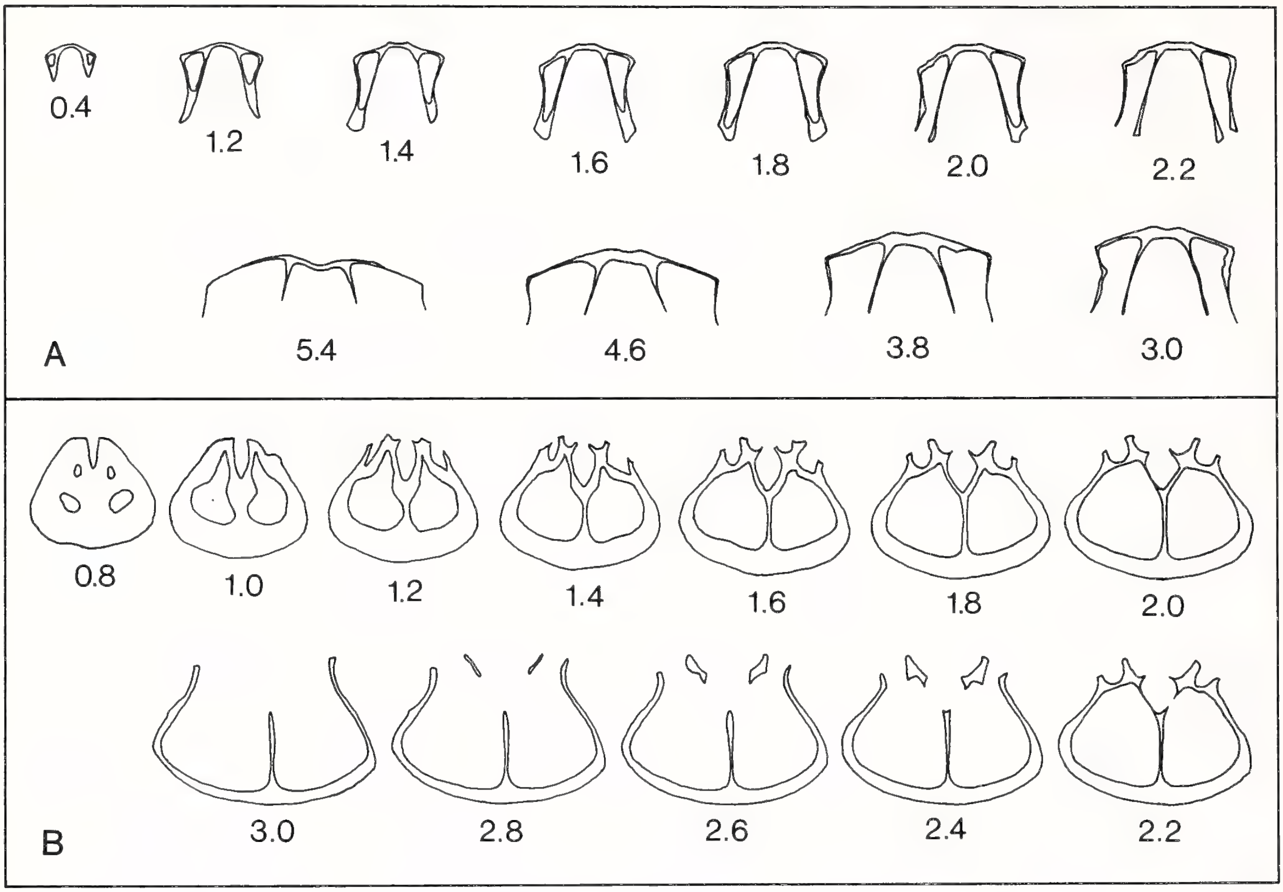


Fig. 13.—Transverse serial sections of *Axiodeaneia glenparkensis* n. sp. from SL396. A, medium sized pedicle valve, CM 34687; B, medium sized brachial valve, CM 34688, both ×3. Numbers refer to distance in mm from beak.

Creek, Pike County, Illinois. One specimen was found at locality SL394.

Family Yunnanellidae Rzhonsnitskaya
Genus **Paraphorhynchus** Weller, 1905

Paraphorhynchus sp.
Fig. 11.36

Remarks.—Three pedicle valves of a coarsely ribbed capillate rhynchonellid, all from SL393, are assignable to the genus *Paraphorhynchus* Weller. The best of these specimens, a small pedicle valve, is illustrated here. The other two specimens consist of fragments of a much larger specimen and a moderate sized specimen. The illustrated specimen is undoubtedly a juvenile and lacks the adult characters needed for specific identification.

Table 20.—*Measurements (in mm) of the types of* Shumardella fracta *n. sp. from SL392.*

Specimen no.	Length	Width	Thickness
CM 34675 (Holotype)	+18.6	23.2	±16.2
CM 34676 (Paratype)	19.4	19.7	15.6
CM 34677 (Paratype)	16.6	18.1	12.9
CM 34678 (Paratype)	15.4	+15.5	10.6
CM 34679 (Paratype)	14.0	15.7	10.6
CM 34680 (Paratype)	10.7	14.2	9.3
CM 34681 (Paratype)	11.6	10.5	9.8

Family Rhynchotetradidae Likharev
Genus **Axiodeaneia** Clark, 1917

Axiodeaneia glenparkensis, new species
Fig. 11.37–11.41, 13

Holotype.—A medium sized brachial valve, Fig. 11.38–11.41, CM 34684, from locality SL396, collected by the author, November 1985.

Paratypes.—A large pedicle valve, Fig. 11.37, CM 34683, from SL397, collected by the author, April 1986; a large brachial valve, not illustrated, CM 34749, same collection as the preceding; a small pedicle valve, not illustrated, CM 34750, same collection as the holotype.

Description.—Medium size for the genus, subequally biconvex; longitudinally guttate in outline; greatest width attained anterior to midlength, usually in anterior third of shell; anterior profile subquadrate; anterior and lateral margins abruptly truncated and strongly serrate, anterior commissure rectimarginate; fold and sulcus lacking; both valves moderately to weakly convex and sloping evenly to truncated margins; both valves with 9 to 12, usually 11 or 12, medium to strong subangular plicae; moderate growth varices irregularly developed in some specimens; micro-ornament consisting of flattened bifurcating capillae, especially prominent in the interplical furrows, and fine irregularly spaced growth lines.

Pedicle valve somewhat less convex than brachial valve; greatest thickness near midlength; umbonal region narrow, not swollen, subtending an apical angle of less than 90 degrees, usually about 66 to 72 degrees; beak small, acute, almost straight; foramen small, incised, continuous with apex of delthyrium; delthyrium and deltidial plates not observed; beak ridges very sharp, angular, extending forward to midlength, defining long high moderately concave palintropes; two medial plicae originating near beak, other plicae originating by intercalation anterior to beak; outermost lateral plicae sometimes very weakly expressed on ventral surface but producing strong deflections at lateral commissures; interior with strong wide teeth and strong, slightly diverging dental plates that converge slightly to valve floor (see Fig. 13A); muscle field not observed in transverse sections.

Brachial valve moderately thicker than opposite valve, sometimes with strong median plica originating in umbonal region (holotype lacks median plica in umbo); umbo moderately or weakly convex, well delimited by subangular beak ridges that also define large concave palintropes that extend forward to near midvalve; otherwise similar to opposite valve externally; interior with deep open septalium, becoming about as wide as deep anteriorly, supported by strong high median septum that extends forward from one-third to one-half valve length; inner socket ridges high, strong, becoming rounded anteriorly; outer hinge plates narrow, almost obsolete; inner hinge plates absent; crural bases flattened, thick, directed dorso-medially in transverse section posteriorly; distal portions of crura not observed.

Distinguishing characters.—This species can be differentiated by its guttate outline, 11 or 12 plicae per valve, apical angle of about 66 to 72 degrees, and very long concave palintropes on both valves defined by angular beak ridges. Internally, the inner hinge plates are nearly obsolete and the dorsal septum extends forward from one-third to one-half the valve length.

Remarks.—*Axiodeaneia glenparkensis* n. sp. is most similar to the type species of the genus, *Axiodeaneia platypleura* Clark, 1917, from the Lodgepole Limestone of Montana. The latter differs in its fewer ribs, less angular shorter beak ridges, and much smaller palintropes on both valves. *Rhynchotetra elongatum* Weller, 1914, from the Pierson Limestone of southwestern Missouri is very similar to the type species and may be distinguished in the same manner. *Axiodeaneia usheri* (Brown), from the Banff Formation of Alberta, is much larger, thicker, has a subovate outline, and is not easily confused with *Axiodeaneia glenparkensis* n. sp.

Table 21.—*Measurements (in mm) of the types of* Axiodeaneia glenparkensis *n. sp.*

Specimen no.	Locality	Length	Width	Thickness	Rib no.
Brachial valves					
CM 34684	SL396	22.3	17.5	7.8	11
CM 34749	SL397	25.1	18.9	13.6	12
Pedicle valves					
CM 34683	SL397	27.0	+22.0	±8.8	9
CM 34750	SL396	20.4	19.3	6.5	12

Distribution.—*Axiodeaneia glenparkensis* n. sp. has been found at only three localities in the Glen Park Formation. The largest collection, from SL 396, consists of 15 specimens, including seven brachial valves, four pedicle valves, and four large fragments. A second smaller collection, from SL397, is comprised of one large pedicle valve, one large brachial valve, and one large fragment. Weller and St. Clair (1928:161) reported the presence of an undescribed *Rhynchotetra* from SL520 that undoubtedly is this species.

Order Uncertain

Superfamily Rhynchoporacea Muir-Wood

Family Rhynchoporidae Muir-Wood

Genus **Rhynchopora** King, 1865

Rhynchopora hamburgensis Weller, 1910

Fig. 9.1–9.16, 11.50–11.57, 14

*1910 *Rhynchopora hamburgensis* Weller, p. 515, fig. 17.
v*1914 *Rhynchopora hamburgensis* Weller: Weller, p. 228–230, pl. 29, fig. 19–30, text-fig. 20.

Lectotype.—Designated herein, FMNH UC7742, illustrated here, Fig. 9.1–9.4, illustrated by Weller (1914:pl. 29, fig. 19–22), from locality SL395.

Paralectotypes.—Fifteen in all, FMNH UC7742, including two complete specimens illustrated here, Fig. 9.5–9.12, and illustrated by Weller (1914:pl. 29, fig. 23–30), same collection as the lectotype.

Diagnosis.—Small rhynchoporids, usually wider than long, with subtrigonal to subpentagonal outline, three to six (usually four or five) rounded to subangular costae in the sulcus, and five to eight (usually five to seven) subangular costae on the flanks.

Remarks.—In general, Weller's (1914) description of this species is accurate for the collection of syntypes. The variability in outline, degree of inflation, and number of ribs, especially on the flanks, is worth noting here. Weller described the species

Table 22.—*Measurements (in mm) of the lectotype, two paralectotypes, and three other illustrated specimens of* Rhynchopora hamburgensis *Weller, 1910, from the Glen Park Formation of Missouri and Illinois.*

Specimen no.	Locality	Length	Width	Thickness	Ribs/ sulcus	Ribs/ flank
Lectotype FMNH UC7742	SL395	+10.8	12.2	8.6	5	7
Paralectotype FMNH UC7742	SL395	10.2	11.5	8.7	5	5
Paralectotype FMNH UC7742	SL395	9.3	9.7	5.8	3	6
Referred specimens						
CM 34670	SL392	8.1	9.0	6.7	4	5
IGS 80P56	SL511	10.4	10.5	5.4	4	7
IGS 80P57	SL511	9.1	9.5	5.7	5	7

as having about five ribs on each flank. This is true for many of the syntypes but the specimen chosen here as lectotype has seven costae on the flanks, and one other syntype illustrated here (Fig. 9.9–9.12) has six. Fifty-one percent of the studied specimens from other localities had seven costae on each flank and 86 percent of these specimens had more than five costae on each flank.

Weller's description of the interior is satisfactory except for the following items. The hingeplate or connectivium is perforated posteriorly as in all other species of this genus (see Fig. 14, section 1.0). The connectivium bears a median ridge for muscle attachment posteriorly but becomes ventrally convex anteriorly and extends well forward of the sockets. The crura are typically rhynchoporid, curving ventrally and becoming comma-shaped, arcuate, or troughlike anteriorly.

Rhynchopora hamburgensis Weller is not very similar to other Mississippian rhynchoporids in North America. It is much smaller than most other species and that feature, plus its ribbing pattern, allows easy differentiation from most other taxa. *Rhynchopora pustulosa* (White), from the McCraney Limestone at Burlington, Iowa, is almost as small as *Rhynchopora hamburgensis* Weller but has fewer, coarser costae and a more subovate outline.

Distribution.—This is one of the most abundant and widely distributed species in the Glen Park Formation, being present in countless numbers at several localities. It is common at all of the localities discussed in this report except for localities SL392 and SL394, which share a distinctive low diversity facies controlled fauna of only a few species.

Table 23.—*Measurements (in mm) of the types of* Rhynchopora prisca *n. sp. from locality SL393.*

Specimen no.	Length	Width	Thickness	Costae	
				Flanks	Fold/ sulcus
Brachial valves					
Holotype					
CM34685	16.2	20.6	8.0	8	8
Paratypes					
IGS 80P52	10.3	12.4	3.6	7	8
IGS 80P53	9.0	10.4	2.9	10	7
Pedicle valves					
IGS 80P54	14.0	13.8	7.5	8	6
IGS 80P55	10.5	10.8	4.9	11	6

Rhynchopora prisca, new species

Fig. 11.42–11.49

Holotype.—A brachial valve, CM 34685, Fig. 11.42–11.43, from locality SL393, collected by the author in April 1985.

Paratypes.—Two pedicle valves and two brachial valves, IGS 80P52 through 80P55, from locality SL393, Fig. 11.44–11.49, collected by C. Collinson.

Description.—Medium sized to large for genus, transversely subovate to subquadrate in outline, unequally biconvex; greatest width attained near or anterior to midlength; anterior commissure uniplicate and serrate; fold low, broad, flattened anteriorly; sulcus shallow, broad, with flattened or weakly concave floor and strongly deflected tongue; surface multicostate with 7 to 11 simple subangular costae on each flank, usually 8 or 9, and 6 or 7 in the sulcus or 7 or 8 on the fold; growth varices moderately strong, irregularly spaced; shell substance finely punctate.

Pedicle valve moderately to weakly convex posteriorly, sloping steeply near lateral margins, curving normal to lateral commissure anteriorly to form moderately large tongue; umbonal region slightly inflated, moderately narrow in small specimens, becoming broad in adults; beak small, suberect or slightly incurved; weak low beak ridges extending laterally from beak, defining narrow palintropes; interior with short slender divergent dental plates; other internal details not observed.

Brachial valve much more convex than pedicle valve, inflated anteriorly; dorsum weakly concave posteriorly in umbonal region then becoming flattened anteriorly on fold; umbonal region broad, weakly convex, not inflated, defined by shallow concave flexures, compressed laterally and forming narrow flanges; beak small, slightly incurved; fold poorly defined posteriorly, rising slightly anteriorly, remaining low throughout, becoming much broader anteriorly; flanks sloping evenly and steeply to lateral margins in small specimens, vertically truncated in large specimens; interior with long slender median septum extending forward for about one-third valve length; other internal details not observed.

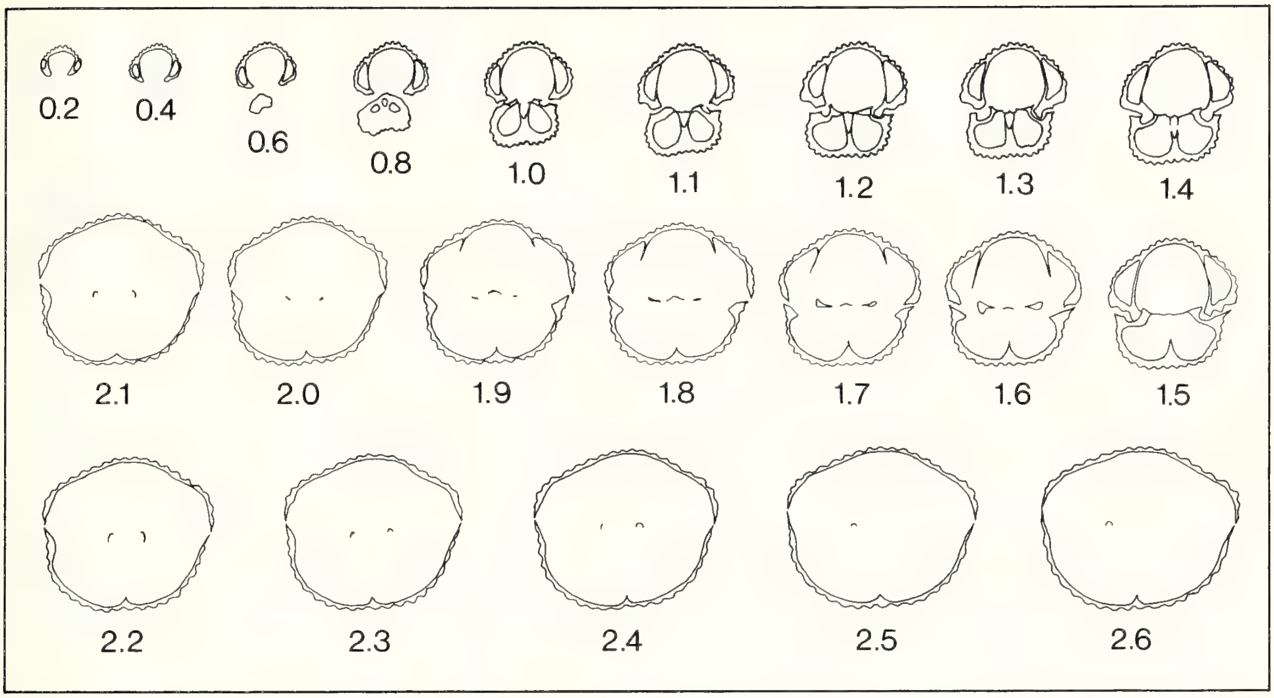


Fig. 14.—Transverse serial sections of *Rhynchopora hamburgensis* Weller from SL511, IGS 80P58. Numbers refer to distance in mm from ventral beak. ×4.

Distinguishing characters.—This species is characterized by its large size and broadly subovate to subquadrate outline, seven to 11, usually eight or nine, coarse subangular costae on each flank, and six or seven costae in the sulcus or seven or eight on the fold; the fold and sulcus are flattened and the dorsum bears a shallow concave sulcus posteriorly.

Remarks.—Its greater size and more numerous costae serve to distinguish this species from the smaller subtrigonal *Rhynchopora hamburgensis* Weller with which it occurs. Small specimens of *Rhynchopora prisca* n. sp. are similar in outline to large specimens of *Rhynchopora hamburgensis* Weller but have more costae on the flanks. *Rhynchopora prisca* n. sp. is not closely similar to other previously described Mississippian rhynchoporids in North America. Some smaller specimens bear general similarity in outline to *Rhynchonella cooperensis* Shumard, 1855, from the Chouteau Limestone of Missouri but the latter, according to Weller (1914:237), has fewer costae and may not be punctate.

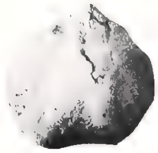
Distribution.—This description is based on a single collection of nine specimens from locality SL393. All of the specimens are disarticulated, there being five brachial and four pedicle valves.

Order Athyridida Boucot, Johnson and Staton
Suborder Athyrididina Boucot,
Johnson and Staton
Superfamily Athyridacea Davidson
Family Meristidae Hall and Clarke
Subfamily Camarophorellinae Schuchert
Genus ***Camarophorella*** Hall and Clarke, 1893

Camarophorella cf. ***C. buckleyi*** (Rowley, 1908)
Fig. 15.32–15.39

1865 *Spirigera missouriensis* Winchell, p. 117 (not Swallow, 1860).
v*1908 *Seminula buckleyi* Rowley, p. 79, pl. 17, fig. 48–53.
v.1914 *Camarophorella missouriensis* (Winchell): Weller, p. 460–462, pl. 82, fig. 70–79.
v.1943 *Camarophorella buckleyi* (Rowley): Williams, p. 91, pl. 7, fig. 21, 22.
1967 *Camarophorella* cf. *C. buckleyi* (Rowley): Rodriguez and Gutschick, p. 379, pl. 44, fig. 21–24, 37, 38.

Remarks.—A small collection of eight specimens belonging to the genus *Camarophorella* Hall and Clarke was recovered from locality SL393. Several of these specimens have spalled translucent layers of shell material that show the internal structures, as well as the characteristic finely papillose inner surface of the valves which simulates punctation. The two largest specimens are brachial valves as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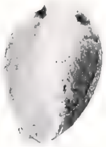
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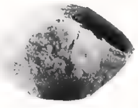
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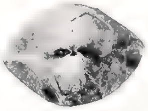
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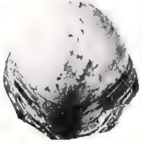
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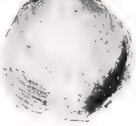
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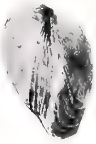
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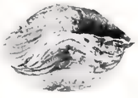
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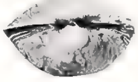
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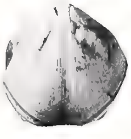
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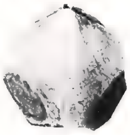
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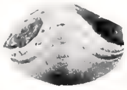
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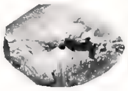
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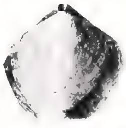
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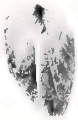
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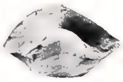
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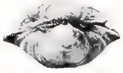
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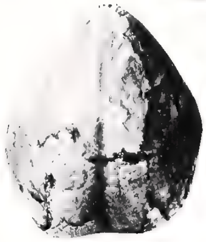
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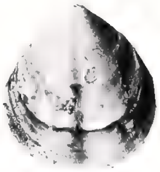
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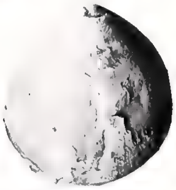
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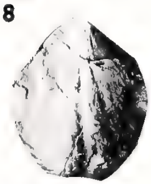
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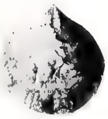
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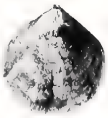
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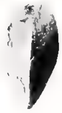
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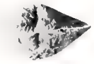
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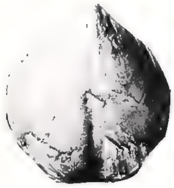
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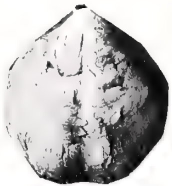
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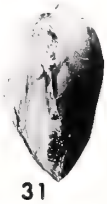
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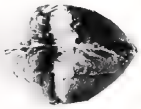
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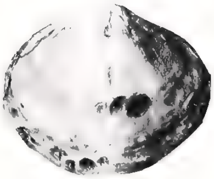
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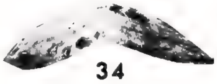
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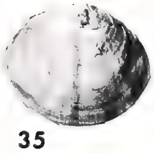
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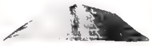
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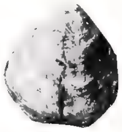
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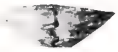
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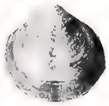
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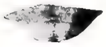
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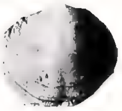
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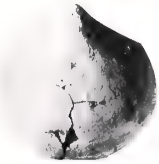
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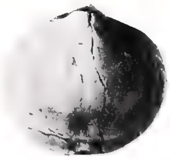
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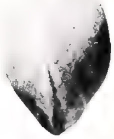
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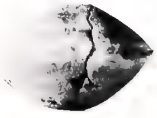
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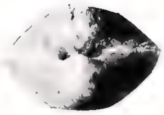
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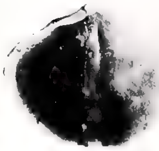
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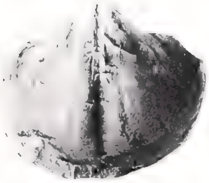
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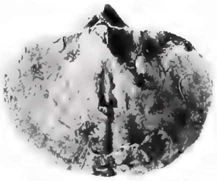
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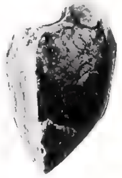
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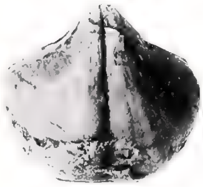
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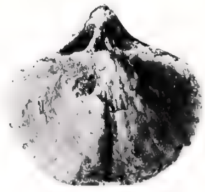
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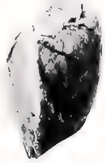
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large as, or slightly larger than, large specimens of authentic *Camarophorella buckleyi* from the Louisiana Limestone. The two pedicle valves illustrated here (Fig. 15.37–15.40) are much smaller than the brachial valves and probably represent juveniles. Their outline is similar to comparably sized growth lines of *C. buckleyi* pedicle valves. In outline, proportions, development of a shallow ventral sulcus, and presence of a shallow narrow medial sinus on both valves, these specimens are similar in most respects to *C. buckleyi* (Rowley). However, certain identification of at least some species of the genus *Camarophorella* requires internal details. The writer was reluctant to destroy any of the few specimens at hand in order to make this determination. Therefore, the specimens are compared with the Louisiana Limestone species, but identification is not certain.

Family Spirigerellidae Grunt
Genus **Composita** Brown, 1849

Composita matutina, new species
Fig. 15.1–15.20, 16

Holotype.—Fig. 15.1–15.5, CM 34689, collected by the author from locality SL393, April 1985.

Paratypes.—Fig. 15.6–15.20, CM 34690–34692, collected by the author from locality SL392, April 1983.

Description.—Medium size for genus, subequally biconvex, slightly elongate, subpentagonal to longitudinally subovate in outline; lateral profile guttate to sublenticular; maximum width attained near midlength; fold and sulcus weakly to moderately developed, anterior commissure uniplicate; ornament simple, consisting only of irregularly spaced growth varices and faint growth lines.

Pedicle valve slightly thicker than brachial valve, most convex in umbonal region, curving evenly to lateral margins; beak small, broad, incurved, subtending an angle of from 97 to 107 degrees; foramen small, rounded, abutting dorsal umbo; delthyrium closed by dorsal valve; venter slightly arched in umbonal region, with shallow rounded sulcus in anterior two-thirds of shell; cardinal extremities moderately broad, rounded, slightly compressed; lateral slopes weakly convex, curving evenly to lateral margins; interior with slender divergent dental plates and wide bladelike teeth; muscle field weakly impressed, longitudinally striated.

Brachial valve most convex in umbonal region, medially arched; flanks weakly convex, sloping evenly to lateral margins; fold very low, poorly delineated only in anterior third or half of valve; cardinal extremities slightly compressed; dorsal umbo slightly tumid; beak small, obscured by delthyrium; interior with broad deep sockets enclosed by very high thin ventro-laterally diverging inner socket ridges that enclose medial edges of teeth; apically perforate transverse hingeplate attached to inner surfaces of inner socket ridges, extending well forward of sockets; crural bases attached to dorsal edges of inner socket ridges and lateral edges of hingeplate; brachidial details and dorsal muscle field not observed.

Distinguishing characters.—This species is characterized by its subpentagonal outline, weakly to moderately developed fold and sulcus, broad ventral umbonal region and beak which subtends an angle of 97 to 107 degrees, and moderately arched dorsum.

Remarks.—*Composita matutina* n. sp. is most similar to the Famennian species, *Composita bellula* Stainbrook, 1947, from the Box Member of the Percha Formation of New Mexico. The latter differs in being larger and less inflated; it is more transverse, and the fold and sulcus are stronger, originating more posteriorly than in *Composita matutina* n. sp. According to Cooper and Dutro (1982:93) *Composita bellula* is the earliest species of the genus *Composita* Brown.

The only other smooth shelled spirigerellid in North American rocks of this age is *Iniathyris corpulenta* (Winchell) from the English River Sandstone of southeastern Iowa. This species is in no way similar to any species of the genus *Composita* because the foramen is presumably lost in adult shells, or at least none has been detected.

←

Fig. 15.—Athyridids and spiriferids. 15.1–15.20, *Composita matutina* n. sp.; 15.1–15.5, ventral, dorsal, lateral, anterior and posterior views of the holotype from SL393, CM 34689; 15.6–15.20, ventral, dorsal, lateral, anterior and posterior views of three paratypes from SL392, CM 34690–34692, all ×1. 15.21–15.32, *Cardiothyris pristina* n. sp.; 15.21, 15.22, two pedicle valves, CM 34693, 34694; 15.23, 15.24, two brachial valves, CM 34695, 34696; 15.25–15.28, ventral, dorsal, lateral and anterior views of a small complete shell, CM 34697; 15.29–15.32, ventral, dorsal, lateral and anterior views of the holotype, CM 34698; all from SL397; all ×2. 15.33–15.40, *Camarophorella* cf. *C. buckleyi* (Rowley); 15.33–15.36, dorsal and anterior views of two brachial valves, IGS 80P59, 80P60; 15.37–15.40, ventral and anterior views of two small pedicle valves, IGS 80P61, 80P62; all from SL393; all ×1.5. 15.41–15.48, *Nucleospira minima* Weller; 15.41, a small brachial valve from SL397, Weller Collection, paralectotype FMNH UC11349; 15.42, a medium brachial valve from SL397, Weller Collection, the lectotype, FMNH UC11349; 15.43–15.47, ventral, dorsal, lateral, anterior and posterior views of a large complete specimen from SL395, CM 34699; 15.48, interior view of a large pedicle valve from SL395, CM 34700; all ×3. 15.49–15.54, *Crurithyris* cf. *C. levicula* (Rowley), ventral, dorsal and lateral views of two spalled but otherwise complete specimens from SL392, CM 34701, 34702, ×4.

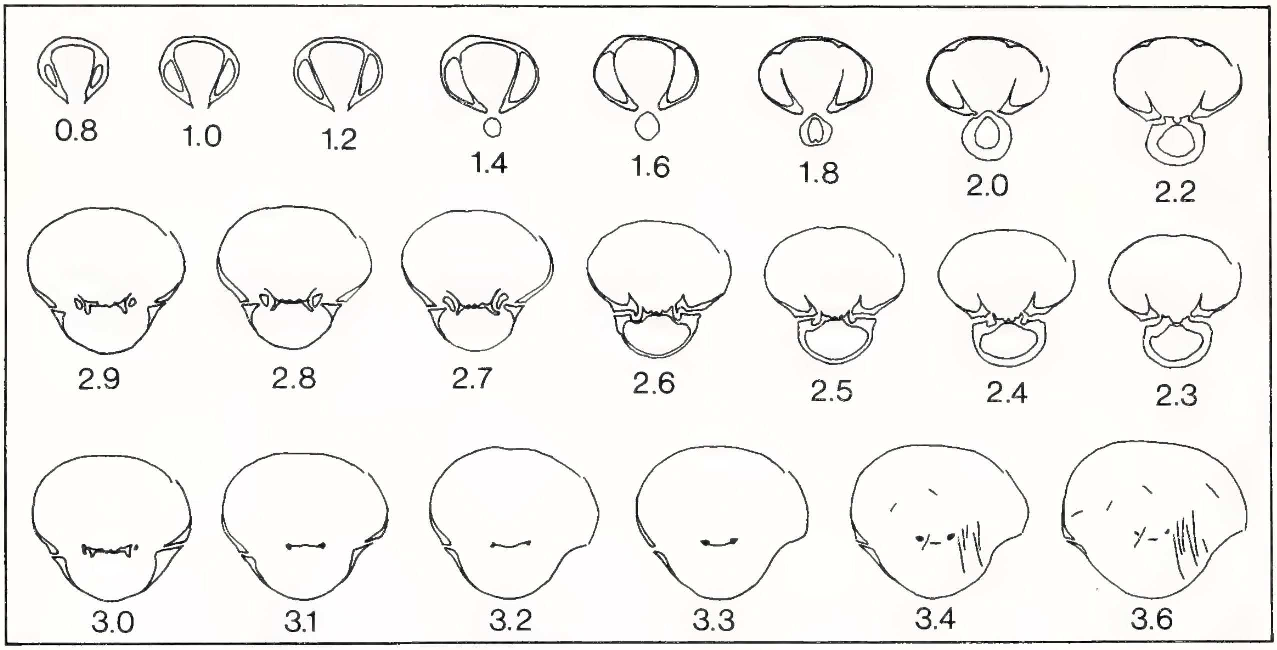


Fig. 16.—Transverse serial sections of *Composita matutina* n. sp. from SL392, CM 34703. Numbers refer to distance in mm from ventral beak. ×2.

Distribution.—*Composita matutina* n. sp. has been found at only two localities in the Glen Park Formation. The holotype and three other disarticulated pedicle valves were found at Brown Branch, Pike County, Illinois, SL393. Ten other specimens, including the three paratypes, are from Horton Creek, Pike County, Illinois, SL392.

Table 24.—*Measurements (in mm) of the types of* Composita matutina *n. sp. from the Glen Park Formation of Illinois.*

Specimen no.	Locality	Length	Width	Thickness
CM 34689	SL393	20.7	20.2	14.3
CM 34690	SL392	19.7	18.5	12.6
CM 34691	SL392	18.1	+17.2	12.1
CM 34692	SL392	16.4	16.3	10.0

Genus *Cardiothyris* Roberts, 1971

Cardiothyris pristina, new species

Fig. 15.21–15.32, 17

Holotype.—Fig. 15.29–15.32, CM 34698, collected by the author from locality SL397, April 1986.

Paratypes.—Two pedicle valves, two brachial valves, and one small complete shell, Fig. 15.21–15.28, CM 34693–34697, respectively, same collection as the holotype.

Description.—Medium size for genus, almost equally biconvex, outline longitudinally subovate to guttate; greatest width attained near midlength; lateral profile sublenticular to subguttate; anterior commissure rectimarginate; fold lacking but weak sulcus developed in each valve producing slightly emarginate anterior margin; cardinal margins almost straight or weakly convex or concave; antero-lateral margins rounded; ornament simple, consisting of irregularly spaced growth varices.

Pedicle valve moderately inflated, most convex in umbonal region; maximum thickness attained slightly posterior to midlength; umbonal region of moderate breadth, beak small, short, subtending an apical angle of from 87 to 95 degrees; foramen small, abutting brachial valve; cardinal margins rounded or very slightly compressed in some specimens; flanks evenly convex; delthyrium occluded by dorsal umbo; sulcus originating in umbonal region as faint medial groove, becoming slightly wider and deeper anteriorly but never becoming well developed; interior with slender, short, moderately divergent dental plates and small broad teeth; other internal details not observed.

Brachial valve closely similar to pedicle valve in outline, profile and proportions; slightly shorter than opposite valve, beak obscured by ventral valve; dorsal sulcus usually slightly weaker than that of opposite valve, sometimes absent or evidenced only by narrow flattened anterior portion of dorsum; interior with apically perforate, broad, flattened hingeplate which is thickly fused to low inner socket ridges; sockets deep and wide; crura and brachidial details not observed.

Distinguishing characters.—This species can be differentiated by its small size, longitudinally subovate to guttate outline, rectimarginate anterior commissure, and a narrow shallow sulcus in each valve.

Remarks.—Bisulcate spirigerellids are rare in the Mississippian of North America. *Composita laevis*

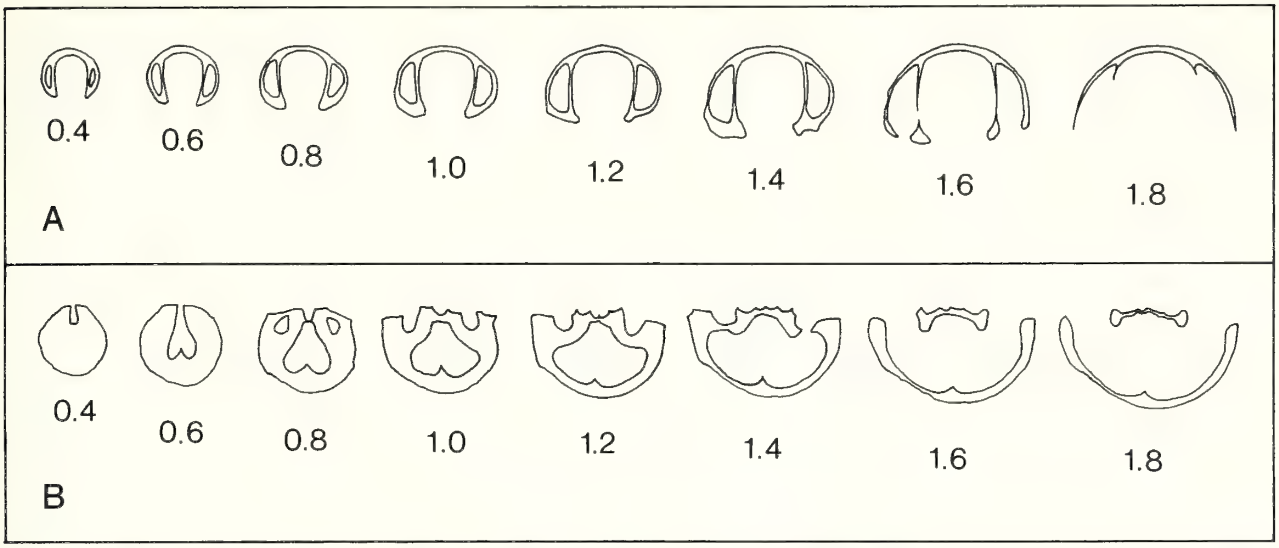


Fig. 17.—Transverse serial sections of *Cardiothyris pristina* n. sp. from SL397. A, medium sized pedicle valve, CM 34704. B, medium sized brachial valve, CM 34705, both ×4. Numbers refer to distance in mm from beak.

Weller, 1914, from Chesterian strata in Kentucky appears to belong in this genus. It is similar in size and the development of a sulcus in each valve but differs from *Cardiothyris pristina* n. sp. in having a more chordate outline with the maximum width being attained well anterior to midlength. A very rare similar species, *Composita lewisensis* Weller, 1914, is said by Branson (1938*a*:76) to be from the Chouteau Limestone of Missouri. It is comparable in size and outline to *Cardiothyris pristina* n. sp. but the ventral sulcus appears to be weaker and a dorsal sulcus, if present at all, is scarcely detectable, resulting in a non-emarginate outline.

Distribution.—*Cardiothyris pristina* n. sp. is found in abundance at locality SL397, Glen Park Quarry, Jefferson County, Missouri. A small collection of 11 specimens was collected at locality SL396, near Hardin, Calhoun County, Illinois.

Table 25.—*Measurements (in mm) of the types of* Cardiothyris pristina *n. sp. from locality SL397.*

Specimen no.	Length	Width	Thickness
CM 34698	12.3	11.3	7.0
CM 34697	7.5	7.2	3.8
Pedicle valves			
CM 34693	15.7	13.5	4.6
CM 34694	11.4	10.5	3.4
Brachial valves			
CM 34695	12.6	11.7	3.6
CM 34696	11.0	9.6	2.5

Superfamily Nucleospiracea Davidson
Family Nucleospiridae Davidson
Genus *Nucleospira* Hall, 1859

Nucleospira minima Weller, 1906
Fig. 15.41–15.48

v*1906 *Nucleospira minima* Weller, p. 447, pl. 6, fig. 29–30.
1914 *Nucleospira minima* Weller: Weller, p. 456–457, pl. 82, fig. 49–60.
1938*a* *Nucleospira minima* Weller: Branson, p. 138–139, pl. 16, fig. 32, 33.

Lectotype.—Designated herein, Fig. 15.42, a brachial valve, FMNH UC11349; also illustrated by Weller (1906:pl. 6, fig. 29; 1914, pl. 82, fig. 50, 56), from locality SL397.

Paralectotypes.—Five brachial valves, FMNH UC11349. The best of these is illustrated here, Fig. 15.40–15.41, same collection as above.

Emended description.—Small for the genus, strongly and subequally biconvex, slightly to moderately wider than long, outline subcircular, lateral profile thickly lenticular to guttate; anterior profile evenly lenticular; narrow shallow median sulcus very poorly developed on both valves, sometimes almost obsolete, producing slightly truncated anterior margin, but not emarginate; anterior commissure rectimarginate; strong irregularly spaced growth varices present but no other ornamentation observed.

Pedicle valve moderately longer and thicker than brachial valve with beak and ventral umbo extending moderately posterior to hingeline; greatest convexity in umbonal region, flanks sloping evenly to lateral and anterior margins; cardinal margins slightly compressed; beak moderately broad and long, suberect; beak ridges angular, short, defining narrow concave interareas; delthyrium small, forming equilateral triangle, with small subdel-

Table 26.—*Measurements (in mm) of* Nucleospira minima *Weller, 1906, from the Glen Park Formation of Missouri and Illinois.*

Specimen no.	Locality	Length	Width	Thickness
Brachial valves				
Lectotype				
FMNH UC11349	SL397	4.6	5.3	2.0
Illustrated paralectotype				
FMNH UC11349	SL397	4.2	4.6	1.9
Other paralectotypes				
FMNH UC11349	SL397	5.3	6.3	2.5
FMNH UC11349	SL397	4.4	4.9	2.2
FMNH UC11349	SL397	4.2	4.4	1.6
FMNH UC11349	SL397	+4.2	+4.3	1.6
Complete referred specimen				
CM 34699	SL395	7.2	7.4	4.9
Referred pedicle valve				
CM 34700	SL395	6.7	8.1	2.7

thyrial plate at apex; deltidial plates not observed; development of sulcus variable, when present, sulcus originating in umbonal region as narrow shallow depression or groove, becoming broader but remaining shallow throughout; in some specimens no discernible sulcus is produced, only a medial flattening being present; interior with long low median ridge extending forward from subdelthyrial plate to about midlength.

Brachial valve substantially shorter and slightly thinner than opposite valve with transversely subovate outline; maximum thickness attained posterior to midlength of valve; umbonal region slightly swollen; beak small and inconspicuous; cardinal margins slightly compressed; flanks sloping evenly to anterolateral margins; development of sulcus similar to that of pedicle valve; interior with long median ridge that extends forward almost to anterior margin; other internal details unknown.

Distinguishing characters.—This species is characterized by its subcircular outline, inflated almost evenly biconvex lateral profile, moderately broad elongate ventral beak, and very weak sulci in both valves.

Remarks.—The lectotype chosen here appears to be a brachial valve, as do all of the specimens in the type suite. Weller (1906, 1914) obviously described some of them as pedicle valves, unless specimens have been lost from the type collection. The description above is based on both the type suite of small brachial valves and the larger specimens from locality SL395, one of which is complete, the other being a large pedicle valve showing interior details. The latter two show the pedicle valve to be quite different in proportions and shape from Weller's description and for this reason an emended description is proposed.

Nucleospira minima Weller is most similar in outline and profile to *Nucleospira hammondi* Branson, 1938, from the Northview Shale of southwestern Missouri. The latter differs in being larger, slightly more elongate, with a stronger ventral sulcus. *Nucleospira obesa* Rowley, 1900, from the lower Burlington Limestone of Pike County, Missouri, also has a subcircular outline and very weak sulci in both valves. It differs from *Nucleospira minima* Weller in having a narrower, shorter ventral beak and less gibbous umbones.

Distribution.—This rare species has been found at only three localities in the Glen Park Formation. The type suite of six brachial valves was collected by Weller from locality SL397. The author has collected only three additional specimens from the same locality. Two specimens were found at locality SL396 and three specimens at locality SL395.

Order Spiriferida Waagen
Suborder Spiriferidina Waagen
Superfamily Cyrtiacea Frederiks
Family Ambocoeliidae George
Genus **Crurithyris** George, 1931

Crurithyris cf. **C. levicula** (Rowley, 1900)
Fig. 15.49–15.54

v*1900 *Ambocoelia levicula* Rowley, p. 262–263, pl. 5, fig. 12–14.

Diagnosis.—Small transverse unequally biconvex crurithyrids with a narrow ventral umbo posteriorly extended and weak but distinct medial sulci in both valves.

Remarks.—These Glen Park specimens are similar in shape and size to Rowley's syntypes and differ only in minor details. The Glen Park specimens illustrated here are both spalled, lacking the surficial shell layers. The sulci in the brachial valves illustrated here are slightly better defined than those in some *C. levicula* from the Burlington Limestone but this may be due to preservation. Specimens from both formations go through similar ontogenetic allometric growth changes to achieve their final transverse outlines. Juvenile specimens from both formations are narrow and difficult to distinguish from adult specimens of *Ambocoelia minuta* White, from the Louisiana Limestone. Although Rowley (1900) and Weller (1914) did not detect micro-ornament, well preserved specimens from both formations possess the finely spinose micro-ornament characteristic of the genus.

Distribution.—*Crurithyris* cf. *C. levicula* (Rowley) has been found at only two Glen Park Formation localities. The illustrated specimens were taken from a collection of 25 specimens from locality SL392. A small collection of four specimens was obtained from locality SL394.

Genus *Eudoxina* Frederiks, 1929

Type species.—*Spirifer medius* Lebedev, 1912.

Diagnosis.—Medium to large unequally biconvex ambocoelliids with pedicle valve much thicker than brachial valve and rounded outline. Rounded fold and sulcus present but weakly developed and poorly differentiated from flanks in most species. Surface of both valves finely costate or costellate, ribs bifurcating freely. Inner shells layers finely pitted, at least in some species. Micro-ornament seemingly lacking. Pedicle valve interior with distinct dental flanges (delthyrial ridges of other authors), lacking dental adminicula. Ventral muscle field deeply impressed. Brachial valve interior with concave finely striate or fimbriate cardinal process, at least in some species, and high antero-laterally directed inner socket ridges (crural plates of other authors). Crural bases attached to dorsal edges of inner socket ridges (Fig. 19). Weak median ridge and long narrow adductor ridges present in some species. Brachidial details unknown.

Stratigraphic range.—This genus appears to be restricted to beds of early Tournaisian age in both the Soviet Union and the North American midcontinent.

Remarks.—The preceding diagnosis is based both on descriptions of the type species from the Soviet Union and the Glen Park species described below. The brachial valve interior was unknown for many years. In recent years Soviet authors such as Poletaev (1971, 1975), Kalashnikov (1974), and Fotieva (1985) have consistently referred to "crural plates" in the brachial valve of *Eudoxina media* (Lebedev). Transverse serial sections of a brachial valve of the Glen Park species clearly show that thin narrow crural bases are attached to the dorsal edges of very high inner socket ridges, not extending to the floor of the valve except apically. The finely striate concave cardinal process in the North American species is very small and has not been reported in Russian specimens. If the striate cardinal process does prove to be present in the type species and is thus a generic character, it may be necessary to reassign *Eudoxina* to a different family.

Eudoxina subrotunda (Weller, 1914)
Fig. 18.1–18.18, 19

v*1858 *Spirifer subrotundatus* Hall, p. 521, pl. 7, fig. 8. (*non* M'Coy, 1855).
1900 *Spirifer subrotundatus* Hall: Weller, p. 76, pl. 2, fig. 8–10.
1914 *Spirifer subrotundus* Weller, p. 356–357, pl. 50, fig. 15–22.

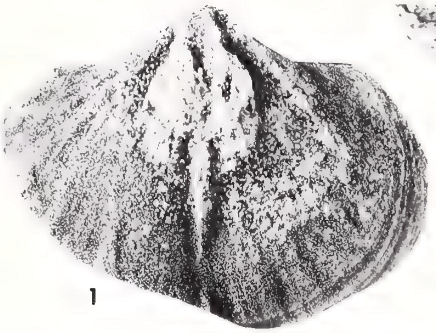
Lectotype.—Designated herein, a very large pedicle valve, UI X-94, Fig. 18.5–18.7, from the English River Sandstone at Burlington, Iowa, collected by A. H. Worthen.

Paralectotype.—A large brachial valve, same locality as above, present location and collector unknown, figured by Hall (1858:pl. 7, fig. 8a).

Diagnosis.—Medium sized *Eudoxina* with broad sloping umbones and shoulders and moderately developed fold and sulcus. Flanks with 25 or more fine flattened costae, many of which bifurcate. Sulcus with ten or more costae similar to those on flanks. Brachial valve interior with deeply concave very finely striate cardinal process, high antero-laterally directed inner socket ridges, and rarely, with very short tabellae.

Remarks.—The satisfactory descriptions of Hall (1858) and Weller (1900, 1914) of the exterior of this well known species were based exclusively on combined internal mold or external cast specimens. That is, external features were impressed upon steinkerns. Information concerning the interior of either valve was not provided by these authors, although many of these sandstone specimens show internal morphology fairly well, especially in both umbones. The four pedicle valves from the Glen Park illustrated here all are composed of original shelly matter but provide no new information concerning the external configuration of this species, including the lack of micro-ornamentation, although one brachial valve shows some indication of fine pitting on a spalled portion of the shell. Internally, Fig. 18.1–18.4 show the lack of dental adminicula, and a deeply impressed ventral muscle field with well differentiated adductor and diductor scars. In the brachial valve very short stout tabellae can be seen supporting the cardinalia, but this character is highly variable in occurrence and probably has little taxonomic significance. The finely striate concave cardinal process and very high inner socket ridges with attached crural bases can be seen in Fig. 19.

Comparisons.—Weller described another species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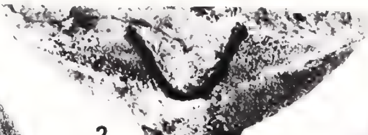
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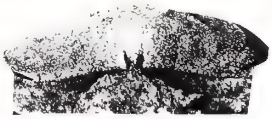
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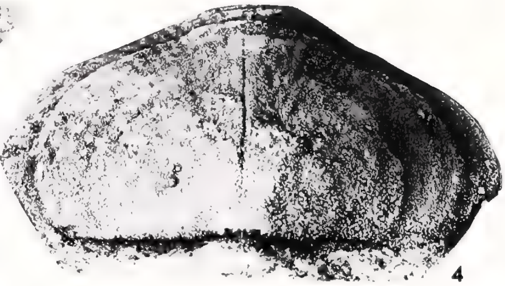
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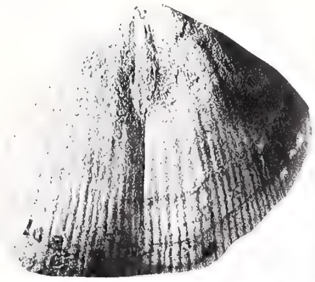
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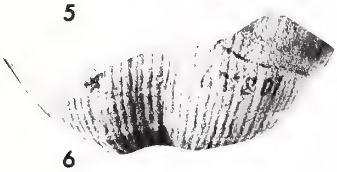
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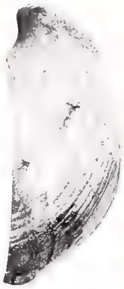
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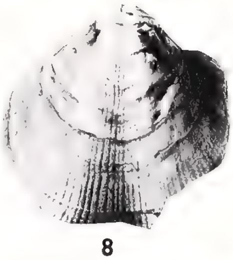
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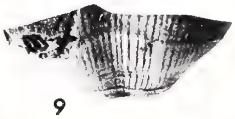
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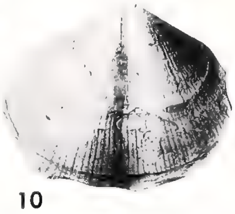
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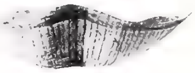
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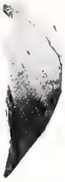
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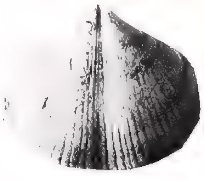
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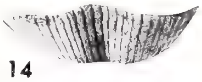
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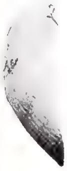
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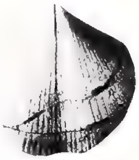
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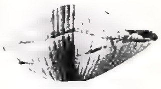
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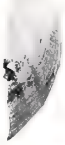
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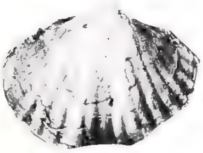
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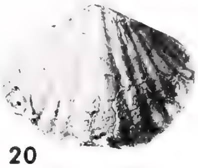
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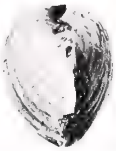
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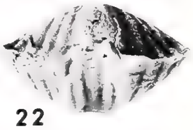
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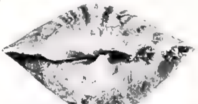
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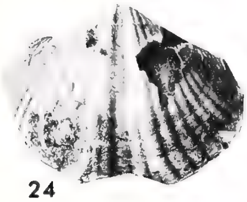
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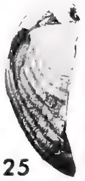
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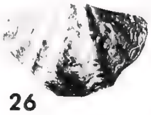
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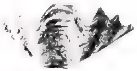
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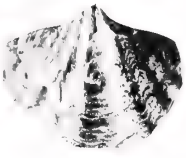
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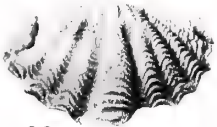
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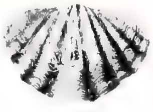
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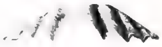
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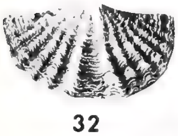
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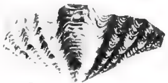
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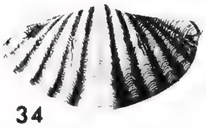
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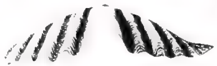
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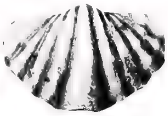
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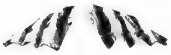
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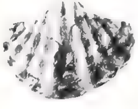
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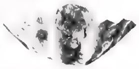
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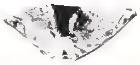
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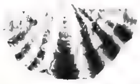
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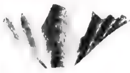
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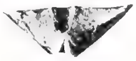
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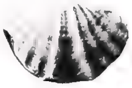
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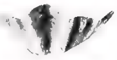
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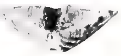
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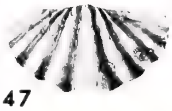
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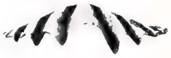
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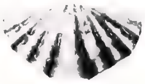
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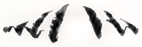
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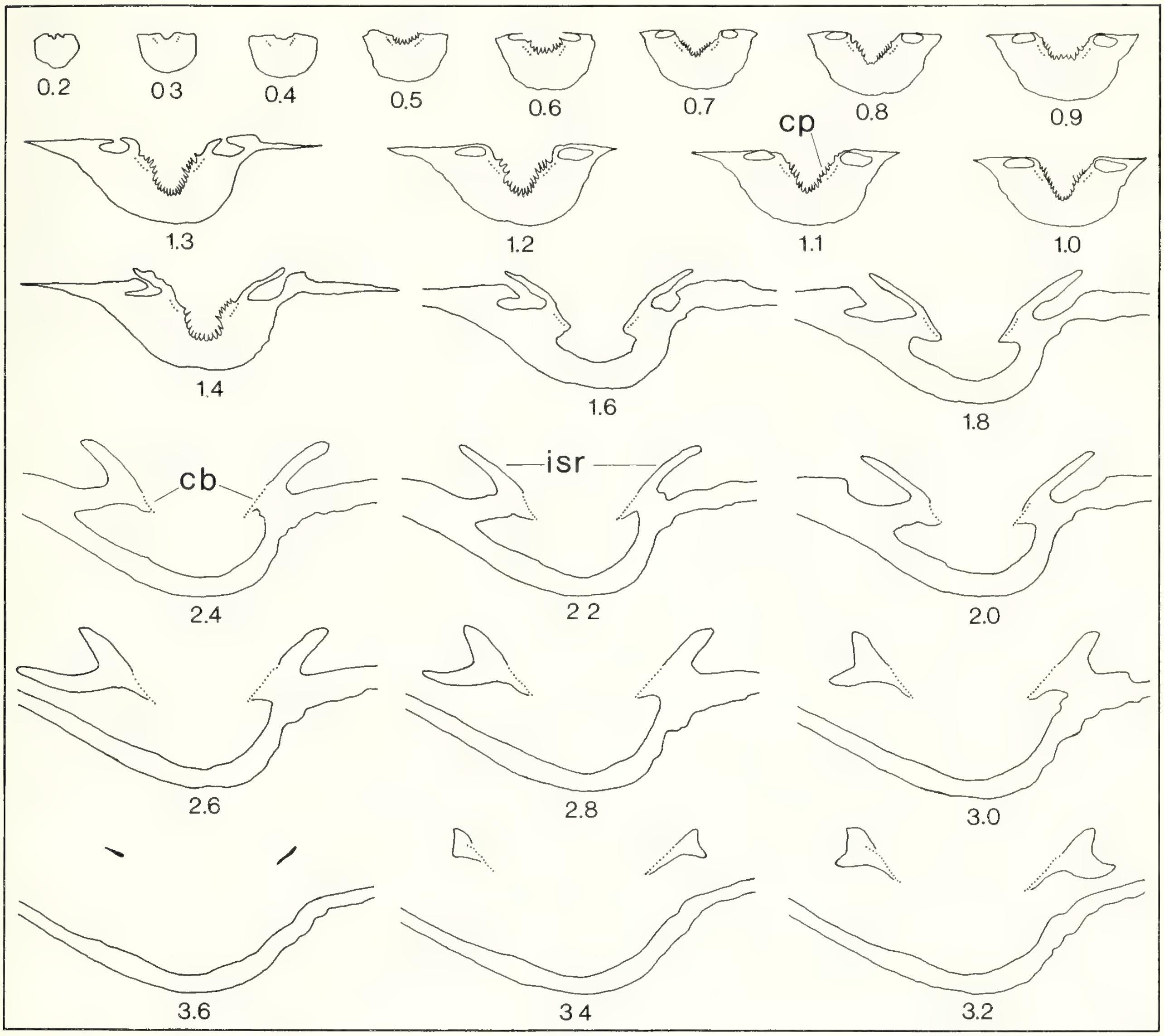


Fig. 19.—Transverse serial sections of a brachial valve of *Eudoxina subrotunda* (weller) from SL393, CM 34755, ×4. (cp = cardinal process, cb = crural base, isr = inner socket ridge.) Numbers refer to distance in mm from dorsal beak.

←

Fig. 18.—Spiriferids. 18.1–18.18, *Eudoxina subrotunda* (Weller); 18.1, 18.2, ventral and posterior views of a sandstone mold of the interior of a pedicle valve from the English River Sandstone at Burlington, Iowa, CM 34706, ×2; 18.3, 18.4, sandstone molds of two brachial valve interiors showing tabellae, from the English River Sandstone at Burlington, Iowa, CM 34707, 34708, ×2; 18.5–18.7, ventral, anterior and lateral views of the lectotype, a very large pedicle valve, UI X-94, Worthen Collection, from the English River Sandstone at Burlington, Iowa, ×1; 18.8–18.18, ventral, anterior and lateral (except no lateral for 18.8) views of four pedicle valves from SL393, IGS 80P63, 80P64, CM 34709, IGS 80P65, respectively, all ×1. 18.19–18.25, *Brachythyris hortonensis* n. sp.; 18.19–18.23, ventral, dorsal, lateral, anterior and posterior views of a small paratype, CM 34710; 18.24, 18.25, ventral and lateral views of the holotype, a large pedicle valve, CM 34711, both from SL392, both ×1. 18.26–18.50, *Tylothyris missouriensis* (Weller); 18.26–18.28, two pedicle valves, paralectotypes, FMNH UC11351, from SL397; 18.29–18.31, two brachial valves from SL397, a paralectotype and the lectotype (18.30–18.31); 18.32–18.35, a large pedicle valve and a large brachial valve from SL395, CM 34712, 34713; 18.36, 18.37, 18.47–18.50, dorsal and anterior views of three brachial valves from SL393, IGS 80P66–80P68; 18.38–18.46, ventral, anterior and posterior views of three pedicle valves from SL393, IGS 80P69–80P71; all ×1.5 except 18.28 and 18.29, ×3.

Table 27.—*Measurements (in mm) of the illustrated pedicle valves of* Eudoxina subrotunda *(Weller).*

Specimen no.	Locality	Length	Width	Thickness
Lectotype				
U.I. X-94	Burlington, Iowa	+38.5	+46.4	15.5
Referred specimens				
IGS 80P63	SL393	31.1	+32.5	11.3
IGS 80P64	SL393	27.2	+32.2	8.0
CM 34709	SL393	22.6	27.2	8.5
IGS 80P65	SL393	20.6	22.3	8.3

of this genus, *Eudoxina maplensis* (Weller, 1914), also from the English River Sandstone. It differs from *Eudoxina subrotunda* (Weller) in having subangular lateral extremities, an elongate outline, more weakly developed fold and sulcus, and the flanks curve abruptly to the lateral margins.

Small specimens of the type species of the genus, *Eudoxina media* (Lebedev), from the lower Tournaisian of the Soviet Union and as illustrated by Poletaev (1975:pl. 6, fig. 1, 2, 5), are similar to some medium sized English River and Glen Park specimens, although the ribbing is slightly finer. The largest specimens of *Eudoxina media,* such as those illustrated by Kalashnikov (1974:pl. 52), are much larger than those of *E. subrotunda.* Internally, the Soviet species seemingly lacks a striate cardinal process, or at least one has not been described. The other described Russian species of this genus are less similar to *Eudoxina subrotunda.*

Distribution.—This is one of the most common brachiopod species in the English River Sandstone in the vicinity of Burlington, Iowa. In the Glen Park Formation, it occurs only at locality SL393 where 29 disarticulated specimens have been recovered.

Superfamily Spiriferacea King
Family Delthyrididae Waagen
Subfamily Tylothyridinae Carter
Genus *Tylothyris* North, 1920

Tylothyris missouriensis (Weller, 1906)
Fig. 18.26–18.50

v*1906 *Delthyris missouriensis* Weller, p. 445–446, pl. 6, fig. 23–26.

v.1906 *Delthyris suborbicularis* Weller, p. 446–447, pl. 6, fig. 27–28.

v.1914 *Delthyris missouriensis* Weller: Weller, p. 302–303, pl. 36, fig. 9–14.

v.1914 *Delthyris suborbicularis* Weller: Weller, p. 303–304, pl. 36, fig. 8.

v.1938*a* *Delthyris clarksvillensis* (Winchell): Branson, p. 137, pl. 16, fig. 9, 10.

v.1938*a* *Delthyris suborbicularis* Weller: Branson, p. 136–137, pl. 16, fig. 12, 13.

?1944 *Tylothyris missouriensis* (Weller): Cooper, p. 323, pl. 122, fig. 11–14.

?1967 *Tylothyris* cf. *T. missouriensis* (Weller): Carter, p. 362, pl. 34, fig. 9.

Table 28.—*Measurements (in mm) of the figured types and other specimens of* Tylothyris missouriensis *(Weller) from the Glen Park Formation of Missouri and Illinois.*

Specimen no.	Locality	Length	Width	Thickness	Ribs/flank
Brachial valves					
Lectotype					
FMNH UC11351	SL397	8.6	13.7	3.9	4
Paralectotype					
FMNH UC11351	SL397	6.1	9.8	2.1	4
Non-type					
CM 34713	SL395	9.6	±20.0	4.9	5
IGS 80P66	SL393	9.7	15.2	4.5	4
IGS 80P67	SL393	8.1	14.7	3.8	4
IGS 80P68	SL393	7.1	13.1	2.5	4
Pedicle valves					
Paralectotypes					
FMNH UC11351	SL397	10.0	12.6	5.2	4
FMNH UC11351	SL397	6.9	8.2	3.8	5
Non-type					
CM 34712	SL395	8.9	15.5	4.5	7
IGS 80P69	SL393	10.3	11.9	4.6	5
IGS 80P70	SL393	8.6	12.3	4.9	5
IGS 80P71	SL393	8.2	11.3	3.9	5

Lectotype.—Designated herein, a brachial valve, Fig. 18.30–18.31, FMNH UC11351, from locality SL397. This specimen was illustrated twice by Weller (1906:pl. 6, fig. 25; 1914, pl. 36, fig. 14).

Paralectotypes.—Eight specimens, FMNH UC11351, including five brachial valves, one illustrated here as Fig. 18.29, and two pedicle valves, both illustrated here as Fig. 18.26–18.28; same collection as the lectotype.

Diagnosis.—Small tylothyrididines with four to seven strong lateral plications, usually five or more, mucronate lateral extremities in large specimens, shallow rounded sulcus and low fold, strongly apsacline to nearly catacline ventral interarea, and crowded lamellose growth lamellae numbering about 2.7 to 4.3 per millimeter on the middle of the flanks.

Remarks.—Small specimens of this species are very difficult to distinguish from small specimens of *Tylothyris clarksvillensis* (Winchell) from the

Louisiana Limestone of Missouri. Both have three or four lateral plicae, slightly rounded lateral extremities, and almost catacline ventral interareas. They can be distinguished, if at all, only by the more crowded growth lamellae in *Tylothyris missouriensis* (Weller). However, large specimens of these species, although rare, are readily differentiated. Large pedicle valves of *Tylothyris missouriensis* (Weller) retain their high angled almost catacline interarea and develop mucronations at the lateral extremities. Large pedicle valves of *T. clarksvillensis* (Winchell), on the other hand, retain their non-mucronate lateral extremities but develop almost orthocline ventral interareas.

In his original description of the Glen Park Limestone faunas, Weller proposed two species of delthyridids, including the species discussed above and another, *Delthyris suborbicularis,* based upon a holotype and one other poor specimen. The holotype differs from most specimens of *Tylothyris missouriensis* (Weller) mainly in the possession of a less inflated pedicle valve, five or six lateral plicae, and a flattened moderately apsacline ventral interarea. Each of these characters is present, alone or in combination, in individual pedicle valves in larger collections of *Tylothyris missouriensis* (Weller). For this reason the writer considers it likely that *Delthyris suborbicularis* Weller is merely a rare morphological variant of *Tylothyris missouriensis* (Weller).

Distribution.—This is a moderately to very common species at the following localities: SL397, SL395, SL393, and SL396. It is rare at SL394 (two specimens).

Family Spiriferidae King
Subfamily Prospirinae Carter
Genus **Parallelora** Carter, 1974

Parallelora nupera, new species

Fig. 20.1–20.42, 21

Holotype.—CM 34715, Fig. 20.6–20.10, collected from locality SL392 by the author, May 1984.

Paratypes.—CM 34714, 34716–34721, Fig. 20.1–20.5, 20.11–20.42, same collection as the holotype.

Table 29.—*Measurements (in mm) of the types of* Parallelora nupera *n. sp. from locality SL392.*

Specimen no.	Length	Width	Thickness	Ribs/ sulcus	Ribs/ flank
CM 34722	31.1	36.9	—	10	27
CM 34714	24.6	27.7	18.4	7	28
CM 34715	22.5	+28.7	19.4	5	26
CM 34716	22.9	27.7	18.9	9	23
CM 34717	18.3	+25.4	13.8	7?	24
CM 34718	18.8	21.3	14.5	6	19
CM 34719	15.1	20.0	11.3	3	21
CM 34720	13.6	17.5	10.4	3	18
CM 34721	9.3	+10.9	6.9	3	14

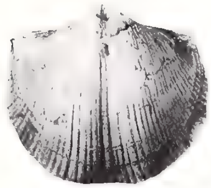
Description.—Medium size for genus, strongly and subequally biconvex; wider than long in all growth stages; outline transversely subovate; lateral extremities mucronate in juveniles, mucronations sometimes suppressed in large adults; maximum width attained at hingeline in juveniles, near midlength in adults; fold and sulcus narrow, shallow; anterior commissure weakly uniplicate; ornament consisting of 23–30 simple or bifurcating rounded costae, usually about 23–25, on the flanks in large adults, and about 5–10, usually 7 or 8, in the sulcus; growth varices irregularly developed; micro-ornament consisting of faint capillae, about 15 per millimeter, and sinuous regularly spaced growth lines.

Pedicle valve moderately inflated, strongly convex in lateral profile, most convex in umbonal region; beak small, incurved; umbonal region moderately broad, projecting posteriorly moderately beyond hingeline; flanks weakly to moderately convex, sloping evenly to antero-lateral margins, except for flexures near cardinal extremities; interarea strongly apsacline to nearly catacline, low, weakly concave, vertically grooved, sharply defined by beak ridges parallel to hingeline; hingeline denticulate; delthyrium slightly narrower than high, partially occluded by stegidial plates; sulcus originating in umbonal region near beak as narrow groove, becoming wider but remaining shallow throughout, flaring slightly near anterior margin; median sulcal costa originating anterior to beak in umbonal region, becoming broader than other sulcal costae anteriorly, often bifurcating near anterior margin in large adults; lateral sulcal costae bifurcating from sulcus-bounding costae and also may bifurcate once in large specimens; lateral costae usually simple, occasionally bifurcating randomly over any portion of flanks, becoming very narrow and faint near lateral extremities; interior with short diverging dental adminicula which fuse with dental flanges at moderately high angle; teeth small, broad; short thick subdelthyrial plate or callus present at apex of delthyrium; muscle field moderately impressed.

Brachial valve slightly thinner than opposite valve, with moderately gibbous umbonal region and inconspicuous beak; dorsum evenly convex, flanks sloping evenly to antero-lateral margins, becoming moderately concave and compressed posteriorly; dorsal interarea very low, defined by angular beak ridges parallel to hingeline, orthocline or slightly apsacline; fold originating at beak as narrow costa defined by fold-bounding grooves that are deeper than intercostal furrows, becoming broader anteriorly but never rising much above flanks; interior with striate cardinal process, wide sockets, and spiralia composed of at least 14 whorls; other internal details not observed.

Distinguishing characters.—This species is characterized by its subovate adult outline, with about 23 to 30 costae on each flank, several of which may bifurcate, and about 5–10 costae in the sulcus, a median sulcal costa that usually bifurcates in adults, and lateral sulcal costae that may bifurcate in large adults.

Remarks.—*Parallelora nupera* n. sp. is similar to *Parallelora marionensis* (Shumard, 1855), from the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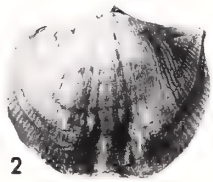
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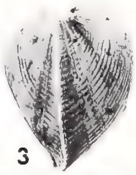
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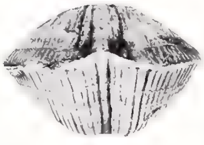
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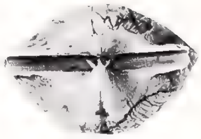
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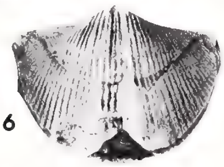
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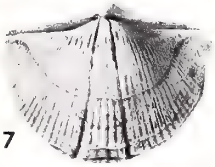
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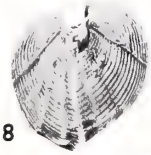
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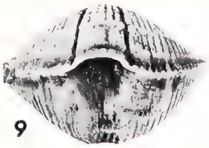
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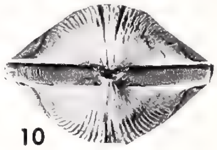
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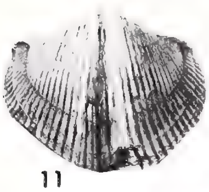
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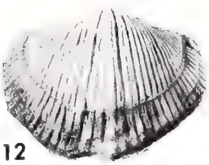
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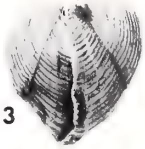
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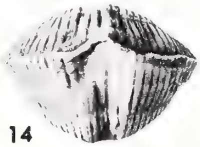
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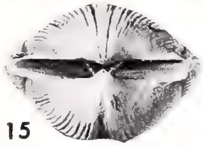
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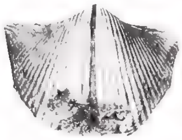
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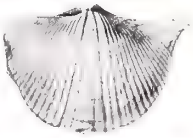
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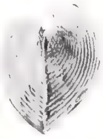
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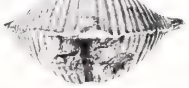
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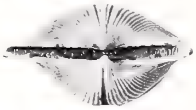
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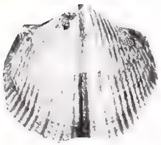
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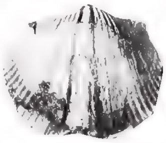
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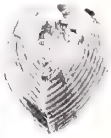
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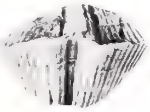
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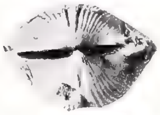
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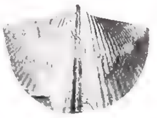
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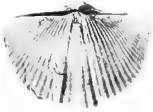
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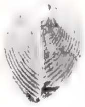
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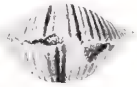
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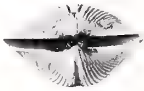
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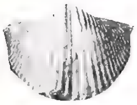
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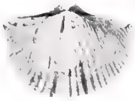
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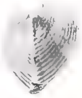
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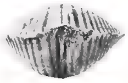
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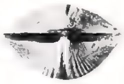
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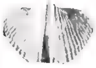
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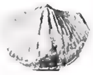
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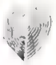
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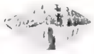
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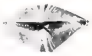
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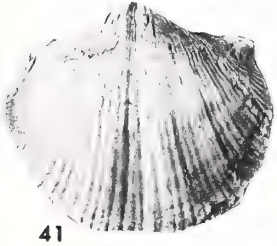
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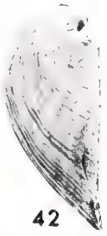
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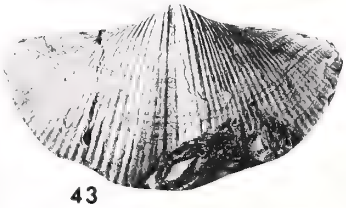
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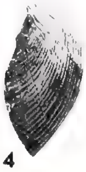
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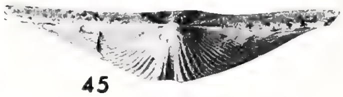
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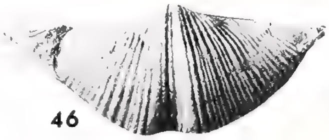
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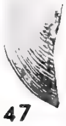
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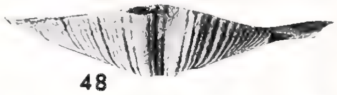
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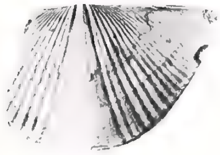
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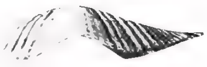
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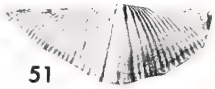
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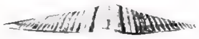
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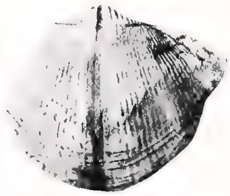
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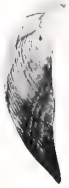
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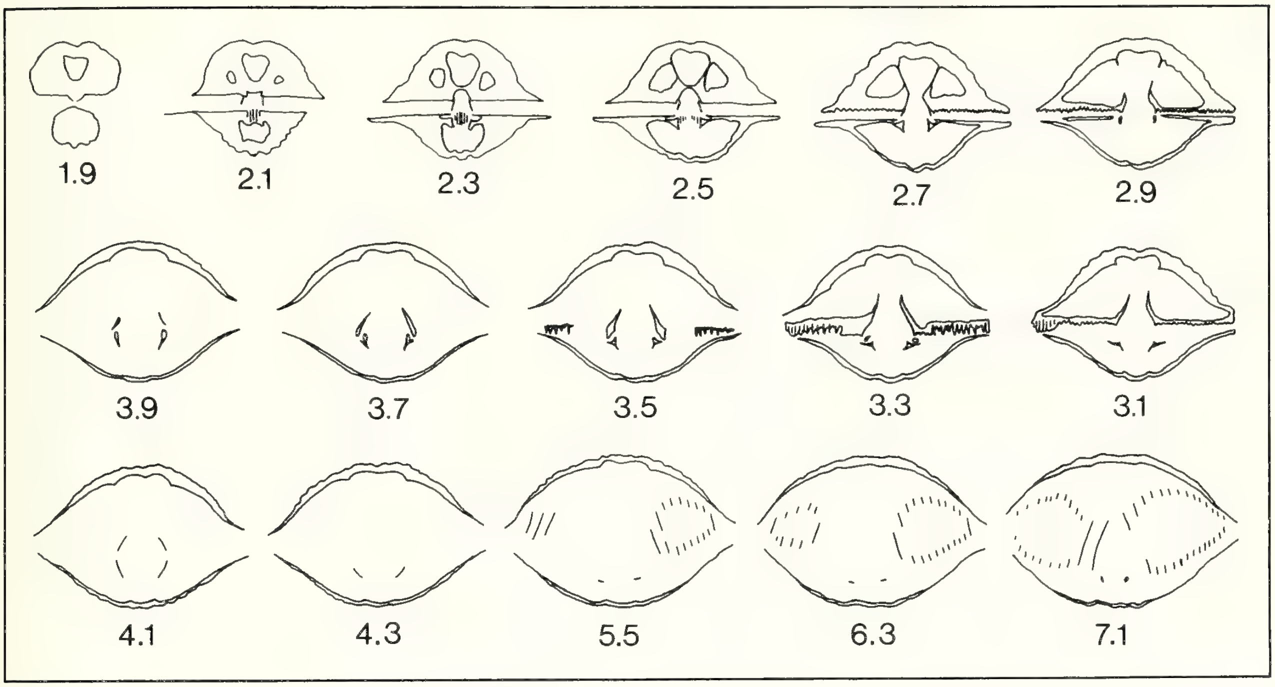

Fig. 21.—Transverse serial sections of *Parallelora nupera* n. sp. from SL392, CM 34724. Numbers refer to distance in mm from ventral beak. ×1.5.

Louisiana Limestone of Missouri and Illinois. The latter differs from *Parallelora nupera* n. sp. in having fewer costae on the flanks, about 20 per flank, and fewer costae in the sulcus, usually three or five. In addition, the median sulcal costa of *P. marionensis* rarely bifurcates, even in the largest shells, and the lateral sulcal costae never bifurcate as far as can be determined by this writer. The outline of *P. marionensis* can be subovate but almost never in the largest shells, which are usually more transverse than large specimens of *Parallelora nupera* n. sp.

Distribution.—This species has very limited distribution in the Glen Park Formation, occurring at only three localities. It is abundant at locality SL392 (110 specimens), and rare at localities SL393 (4 specimens) and SL394 (5 specimens).

Genus ***Unispirifer*** Campbell, 1953

Unispirifer senex, new species

Fig. 20.43–20.54, 22

Holotype.—A large pedicle valve, IGS 80P72, Fig. 20.43–20.45, from locality SL393, collected by C. Collinson.

Paratypes.—Two large pedicle valves and a large brachial valve, IGS 80P73–80P75, Fig. 20.46–20.50, 20.53–20.54, same collection as the holotype; one small brachial valve, CM 34723, Fig. 20.51–20.52, collected by the author from locality SL393.

Description.—Medium size for genus, unequally biconvex with pedicle valve more inflated than brachial valve; outline acutely subtriangular in small adults and juveniles, becoming more elongated and subsemicircular in large adults; greatest width along

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Fig. 20.—Spiriferids. 19.1–19.42, *Parallelora nupera* n. sp.; 19.1–19.40, ventral, dorsal, lateral, anterior and posterior views of a growth series of eight specimens, including the holotype (19.6–19.10), CM 34714–34721, respectively; 19.41, 19.42, ventral and lateral views of a large pedicle valve, CM 34722; all from SL392; all ×1. 19.43–19.54, *Unispirifer senex* n. sp.; 19.43–19.45, ventral, lateral and posterior views of the holotype, IGS 80P72; 19.46–19.48, ventral, lateral and anterior views of a pedicle valve, IGS 80P73; 19.49–19.52, dorsal and anterior views of two brachial valves, IGS 80P74 and CM 34723, respectively; 19.53, 19.54, ventral and lateral views of an elongate pedicle valve, IGS 80P75; all from SL393; all ×1.

Table 30.—*Measurements (in mm) of the types of* Unispirifer senex *n. sp. from locality SL393.*

Specimen no.	Length	Width	Thick-ness	Ribs/fold-sulcus	Ribs/flank
		Pedicle valves			
IGS 80P72	±25.2	45.9	10.7	8	29
IGS 80P73	17.7	45.1	9.0	5	27
IGS 80P75	25.3	±36.0	9.3	7	27
		Brachial valves			
IGS 80P74	20.1	±37.2	6.0	10	+22
CM 34723	11.1	±31.6	4.3	6	24

hingeline in all growth stages; cardinal extremities alate or slightly mucronate, subangular; fold and sulcus narrow and well defined but shallow and weakly developed; anterior commissure weakly uniplicate; ornament consisting of 24–29 rounded costae on each flank in large adults and about 5–10 in the sulcus; costae on flanks mostly simple but commonly with about one to three bifurcating umbonal costae; anterior bifurcations very rare; median sulcal costa simple in small specimens but may bifurcate in large adults; simple lateral sulcal costae bifurcate from sulcus-bounding costae; strong irregularly spaced growth varices present; micro-ornament consisting of faint capillae and sinuous regularly spaced growth lines; shell substance thick in umbonal regions of both valves.

Pedicle valve moderately inflated, most convex in umbonal region with maximum thickness attained near or slightly posterior to midlength; umbonal region moderately broad and protruding moderately posterior to hingeline; beak small, slightly incurved; flanks gently convex, sloping evenly to antero-lateral margins, becoming reflexed and weakly concave near lateral extremities; beak ridges angular, sharply defining ventral interarea; interarea weakly concave, of moderate height, acutely triangular, truncated at lateral extremities, apsacline in small adults, becoming orthocline in large specimens; hingeline vertically grooved, denticulate; delthyrium wide; deltidial plates not observed; sulcus originating as medial groove at beak, becoming rounded anteriorly, remaining shallow for entire length; sulcus-bounding costae of normal size or slightly enlarged; interior with short stout dental adminicula fused with dental flanges at moderately high angle; teeth small; adminicula enclose deeply impressed diductors and raised narrow adductor ridges; thick callus present in entire posterior region.

Brachial valve less inflated than pedicle valve, most convex in umbonal region; flanks gently convex from front to rear, flattened or weakly concave in anterior profile, sloping gently to antero-lateral margins; lateral extremities slightly compressed; dorsal beak tiny and inconspicuous; dorsal interarea not observed; fold originating as narrow costa in umbo, defined only by fold-bounding grooves, becoming broader and rising very little above flanks anteriorly, clearly delineated by disproportionately deep fold-bounding grooves; interior with striate cardinal process composed of numerous thin vertical plates and supported by thick umbonal callus; sockets wide, weakly supported by thin inner and outer socket ridges; brachidial details not observed; dorsal muscle field moderately impressed.

Distinguishing characters.—This species is distinguished by its ontogenic tendency to become more elongated in large specimens with its outline changing from subtrigonal to subsemicircular and its lateral extremities changing from acutely alate or slightly mucronate to subrounded. It is further characterized by its rounded shallow narrow sulcus with a median sulcal costa that may bifurcate in large adults, 24 to 29 lateral costae, several of which may bifurcate in the umbonal region, and a low dorsal fold that is clearly delimited by deep fold-bounding grooves.

Remarks.—*Unispirifer senex* n. sp. bears similarity to both *Spirifer* cf. *S. greenockensis* Brown and the specimens described as *Spirifer* sp.? by Rodriguez and Gutschick (1967:377–379) from the Sappington Formation of Montana. It differs slightly from the first Sappington species in having a slightly narrower fold-sulcus with fewer sulcal costae and the costae on the flanks bifurcate in the umbonal region, not near midlength as in the Sappington species. The other Sappington form, *Spirifer* sp.?, has about 35 lateral costae, many of which bifurcate anterior to midlength, and acutely angular or mucronate lateral extremities in the largest specimens, giving it a very transverse outline, quite unlike *Unispirifer senex* n. sp.

In its tendency toward elongation of the shell in late ontogeny and the presence of a strong median sulcal costa that tends to bifurcate, *Unispirifer senex* n. sp. is similar to *Unispirifer greenockensis* (Brown) from the Banff Formation of Alberta as redescribed by Carter (1987). The latter differs from *Unispirifer senex* n. sp. in having slightly fewer lateral costae, a more poorly defined sulcus with more numerous freely bifurcating lateral sulcal costae and an unusually coarse bifurcating median sulcal costa.

Distribution.—The description given above is based on a single collection of 31 disarticulated valves from locality SL393.

Family Brachythyrididae Frederiks
Subfamily Brachythyridinae Frederiks
Genus *Brachythyris* M'Coy, 1844

Brachythyris hortonensis, new species
Fig. 18.19–18.25

Holotype.—A large pedicle valve, CM 34711, Fig. 18.24–18.25, collected at locality SL392 by the author, May 1984.

Paratype.—A crushed but otherwise complete smaller specimen, CM 34710, Fig. 18.19–18.23, same collection as the holotype.

Description.—Medium size for genus, wider than long, transversely subelliptical in outline, maximum width attained near

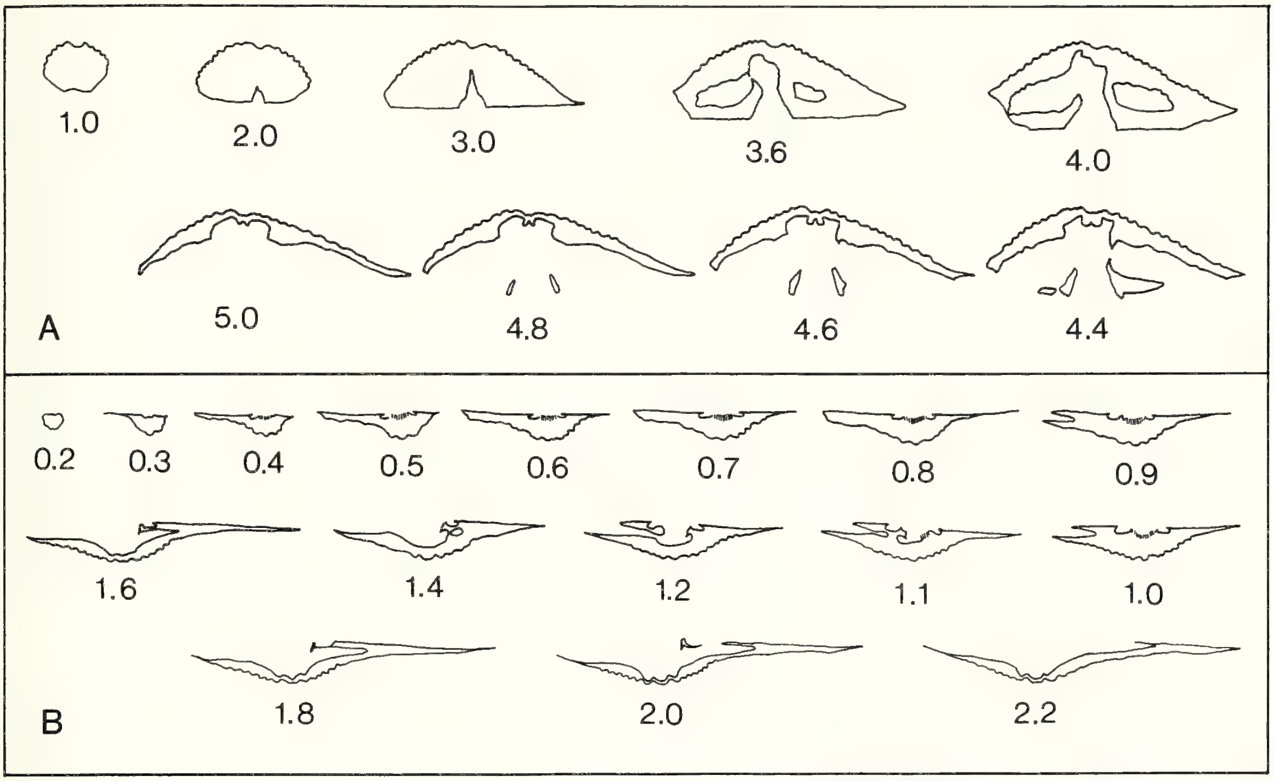


Fig. 22.—Transverse serial sections of *Unispirifer senex* n. sp. from SL393. A, medium sized pedicle valve, IGS 80P76; B, medium sized brachial valve, IGS 80P77, both ×1.5. Numbers refer to distance in mm from beak.

midlength; lateral extremities rounded; fold and sulcus of moderate width; anterior commissure weakly uniplicate; ornament consisting of about 11 coarse rounded simple lateral plicae in large shells, and three or five in sulcus, median costa being broader and more flattened than lateral sulcal costae; micro-ornament, if any, not observed.

Pedicle valve slightly more inflated than brachial valve, most inflated in umbonal region, almost evenly convex in lateral profile; umbonal region broad, extending well posterior to hingeline; beak small, slightly incurved; venter slightly arched, flanks more weakly convex, sloping evenly to antero-lateral margins; lateral extremities defined by slightly concave flexures, moderately compressed; ventral interarea small, concave, acutely triangular, defined by weak beak ridges, apsacline; delthyrium about as wide as high, partially occluded by thin low posteriorly directed deltidial plates; sulcus originating at beak as shallow narrow groove, becoming gradually broader and moderately deeper anteriorly but remaining shallow throughout; median sulcal costa slightly rounded, almost flat, broader than lateral sulcal costae; one or two pairs of lateral sulcal costae originate by bifurcation from sulcus-bounding costae; interior lacking dental adminicula; other internal details not observed.

Brachial valve with slightly gibbous umbo but almost evenly convex in lateral profile; flanks moderately convex, sloping evenly to antero-lateral margins; lateral extremities slightly compressed; fold originating in umbonal region as narrow low plica, becoming broader anteriorly but rising only slightly above flanks at front margin, defined mainly by fold-bounding grooves that are slightly deeper than those of other lateral intercostal furrows; ribbing lacking on fold but distinct medial groove extending from umbonal region to anterior margin; dorsal interarea and internal details not observed.

Distinguishing characters.—This species is characterized by its transversely subelliptical outline, about 11 simple plicae on the flanks, three plicae in the sulcus, with a well defined weakly rounded median sulcal costa, and a distinct dorsal median groove on the fold.

Remarks.—Most other Lower Mississippian species of the genus *Brachythyris* lack a rounded median sulcal costa and can be distinguished on that basis alone. Carter (1987) described a small specimen of similar form to *Brachythyris hortonensis* n. sp. as *Brachythyris* cf. *B. chouteauensis* (Weller) from the Banff Formation of Alberta. Like the Glen Park species this specimen is transversely subovate with

Table 31.—*Measurements (in mm) of the types of* Brachythyris hortonensis *n. sp. from locality SL392.*

Specimen no.	Length	Width	Thickness
Holotype			
CM 34711	24.9	32.7	10.2
Paratype			
CM 34710	20.5	26.9	+15.3

about 11 plicae on the flanks and three in the sulcus. It differs in having broader shoulders, lacks a dorsal median groove in the fold, is much smaller, and the fold is higher at the front.

The common mid-Kinderhookian species, *Brachythyris peculiaris* (Shumard), is not similar to this Glen Park species, having a rhomboidal outline, fewer plicae, and a narrow smooth sulcus, in addition to being much smaller. *Brachythyris chouteauensis* (Weller), of Late Kinderhookian and Early Osagean age, has a much more inflated pedicle valve, broader shoulders, a stronger fold-sulcus, and lacks a median sulcal costa.

Brachythyris hortonensis n. sp. is similar in size, shape and ornamentation to *Brachythyris planulata* Roberts, 1971, from the Ningbing Limestone (Tournaisian) of western Australia. It differs from *Brachythyris hortonensis* n. sp. in having broader shoulders, the median sulcal costa tends to be broader and flatter, and there may be more pairs of lateral sulcal costae.

Distribution.—This description is based on only three specimens, the holotype, a paratype, and a large fragmentary brachial valve, all from locality SL392.

Superfamily Reticulariacea Waagen
Family Elythidae Frederiks
Genus ***Kitakamithyris*** Minato, 1951

Kitakamithyris cooperensis (Swallow, 1860)
Fig. 23.21–23.45

1860 *Spirifer cooperensis* Swallow, p. 643. (types lost)
1900 *Reticularia cooperensis* (Swallow): Weller, p. 80–81, pl. 2, fig. 1.
1914 *Reticularia cooperensis* (Swallow): Weller, p. 428–429, pl. 75, fig. 21–33.
1958 *Reticularia cooperensis* (Swallow): Sanders, p. 58–59, pl. 6D, fig. 21–30.
1967 *Reticularia? cooperensis* (Swallow): Carter, p. 405–408, pl. 40, fig. 1–7; textfig. 41.

Types.—Swallow's types, deposited at the University of Missouri, were lost in a fire in 1892.

Diagnosis.—Medium sized transverse elythiids with a subelliptical outline, weakly developed fold and sulcus, and moderately narrow ventral umbonal region that extends slightly posterior to the hingeline. Internally, both valves bear a low thin median ridge that extends to about midlength.

Remarks.—The synonomy given above is not intended to be complete but is rather a guide to several references that provide complete descriptions of the external and internal morphology of this widely identified species. Also, as noted in the synonomy, Weller (1900) identified this species in the English River Sandstone at Burlington, Iowa. The Glen Park Limestone specimens are closely similar to authentic Chouteau Limestone specimens except for being moderately larger with slightly less protuberent ventral umbones. *Kitakamithyris cooperensis* (Swallow) from the Chouteau varies so much in these parameters they seem to be of little taxonomic importance. As Sanders (1958) and Carter (1967) have pointed out this species lacks a true median septum in the brachial valve but it may have a variably developed low dorsal median ridge. For this reason it is here assigned to the genus *Kitakamithyris* Minato, 1951. *Reticularia setigera* Hall var. *internascens* Girty, 1928, is probably assignable to the genus *Kitakamithyris* Minato. Aside from its much younger age it differs from *Kitakamithyris cooperensis* (Swallow) in being larger, generally more transverse, and, according to Girty (1928:93) the dental plates differ in size and placement.

Distribution.—*Kitakamithyris cooperensis* (Swallow) is not a common fossil in the Glen Park Formation. Only three collections were found at localities SL392 (16 specimens), SL393 (5 specimens) and SL394 (2 specimens).

Family Martiniidae Waagen
Genus ***Eomartiniopsis*** Sokolskaya, 1941

Eomartiniopsis kinderhookensis, new species
Fig. 24.35–24.47, 25

Holotype.—Fig. 24.35–24.38, CM 34737, collected by the author from locality SL392, May 1984.

Paratypes.—Two pedicle valves, Fig. 24.39–24.42, CM 34738, 34739; a large brachial valve, Fig. 24.43, CM 34740; a small shell, Fig. 24.44–24.47, CM 34741; all from the same collection as the holotype.

Description.—Medium size for genus, subequally biconvex, transversely subovate in outline; lateral extremities rounded, hingeline brachythyrid; maximum width attained near or slightly posterior to midlength; fold and sulcus narrow and well developed in most specimens; anterior commissure uniplicate; ornamentation lacking except for irregularly spaced growth varices, faint closely and regularly spaced growth lines, and very weak obscure ribs on flanks of some specimens; spalled surfaces may show faint radial striations or fine dense pits or shagreen ornament; shell substance impunctate.

Pedicle valve most convex in umbonal region; beak small, incurved; umbonal region moderately broad, only moderately extended posterior to hingeline; flanks gently convex, sloping evenly to antero-lateral margins; lateral extremities slightly compressed; sulcus well defined, narrow, rounded, originating at beak, becoming wider and deeper anteriorly, producing moderate tongue; ventral interarea very small, triangular, apsacline, poorly defined by well rounded beak ridges; delthyrium about as wide as high, deltidial plates not observed; interior with thin closely set, slightly diverging dental adminicula that extend foward about one-fourth length of valve; teeth small; ventral muscle field slightly impressed.

Brachial valve usually slightly less inflated than pedicle valve; umbonal region broad, moderately inflated, slightly tumid, protruding posteriorly slightly; dorsal beak tiny, narrow, inconspicuous; dorsal interarea, if present, not observed; flanks as in opposite valve, lateral extremities slightly compressed; dorsum arched; fold originating in umbonal region as weak rounded plica, becoming well defined and rising moderately above flanks at anterior margin, narrow; interior with unsupported striate cardinal process, wide sockets, with medially concave crural bases attached to inner socket ridges; brachidium not observed; dorsal muscle field not impressed.

Distinguishing characters.—This species can be differentiated by its small ventral umbo that protrudes posteriorly very little beyond the hingeline and its well defined narrow fold and sulcus.

Remarks.—Early Kinderhookian *Eomartiniopsis* or similar genera are not reported in North America. *Eomartiniopsis girtyi* (Branson, 1938) from the Chouteau Limestone of central Missouri and the Chappel Limestone of central Texas is much larger, more transverse, has better defined ribbing, a wider fold and sulcus, and the ventral umbo is much more protuberent. *Eomartiniopsis rostrata* (Girty, 1899) from the Lodgepole Limestone of the northern Cordilleran region, the Gilmore City Limestone of northern Iowa, the Banff Formation of Alberta, and the St. Joe Limestone of Arkansas and Oklahoma has a shallow wide poorly defined sulcus with a high wide rounded fold and large ventral tongue. The outline and development of the ventral umbo is highly variable in this species, but it is usually broad, often flattened, and protruding well beyond the hingeline with little evidence of a sulcus or merely a shallow medial groove. Furthermore, the flanks are invariably smooth with no trace of ribbing.

Table 32.—*Measurements (in mm) of the types of* Eomartiniopsis kinderhookensis *n. sp. from locality SL392.*

Specimen no.	Length	Width	Thickness
Holotype			
CM 34737	21.4	21.5	15.7
Paratypes			
CM 34741	17.0	19.2	12.4
Pedicle valves			
CM 34738	22.9	+27.6	+8.3
CM 34739	22.4	+24.1	9.6
Brachial valve			
CM 34740	20.2	25.0	9.0

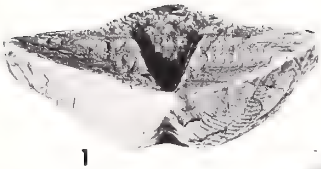
Eomartiniopsis helenae Sokolskaya, 1941, from the Tournaisian of the Moscow Basin (Malevsky Horizon), is similar in outline and in the well-defined narrow fold and sulcus. It differs from *Eomartiniopsis kinderhookensis* n. sp. in having a more protuberent ventral umbo and internally it has short tabellae.

Assignment of this species to the genus *Eomartiniopsis* Sokolskaya, 1941, is arguable. As Brunton (1984*b*:95) has pointed out, there are several martiniid generic names in the literature that possibly could apply to smooth or nearly smooth species with dental adminicula. Two generic names seem to be available for these early Carboniferous species, namely *Eomartiniopsis* Sokolskaya, 1941, and *Merospirifer* Reed, 1948. The former was described as possessing short incipient septal plates but the single thin section illustrating these septal plates (Sokolskaya, 1941:pl. 12, fig. 1b) shows crural bases approaching but not touching the floor of the valve. The type species of this genus, *Eomartiniopsis elongata* Sokolskaya, 1941, must be thoroughly redescribed and illustrated before one can judge the taxonomic significance of these septal plates. *Merospirifer* Reed, 1948, has been recently discussed and reillustrated by Brunton (1984*b*:95–97, fig. 147–149).

→

Fig. 23.—Syringothyridids and reticulariids. 22.1–22.20, *Syringothyris extenuata* (Hall), ventral, dorsal, anterior, posterior and lateral views of four complete but moderately crushed specimens from SL392, CM 34725–34728, ×1; 22.21–22.45, *Kitakamithyris cooperensis* (Swallow), ventral, dorsal, lateral, anterior and posterior views of five specimens from SL392, CM 34729–34733, ×1.

Fig. 24.—Terebratulids and reticulariids. 23.1–23.34, *Hamburgia typa* Weller; 23.1–23.18, ventral, dorsal and lateral views of six small complete shells from SL393, IGS 80P78–80P83, ×3; 23.19, a large pedicle valve showing color banding from SL395, the lectotype, FMNH UC14245, ×1; 23.20–23.34, ventral, dorsal, lateral, anterior and posterior views of three larger complete shells from SL393, CM 34734–34736, ×1. 23.35–23.47, *Eomartiniopsis kinderhookensis* n. sp.; 23.35–23.38, ventral, dorsal, lateral and anterior views of the holotype, CM 34737; 23.39–23.42, ventral and anterior views of two pedicle valves, CM 34738, 34739; 23.43, a large brachial valve, CM 34740; 23.44–23.47, ventral, dorsal, lateral and anterior views of a small nearly complete shell, CM 34741; all from SL392; all ×1.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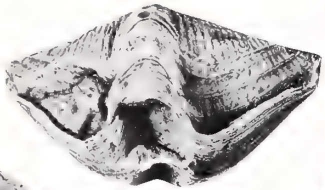
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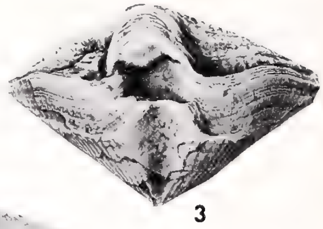
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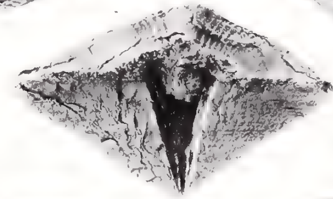
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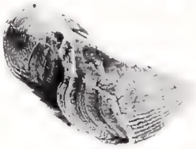
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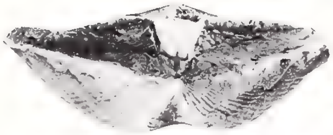
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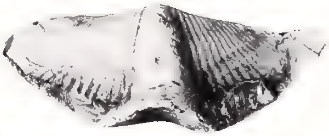
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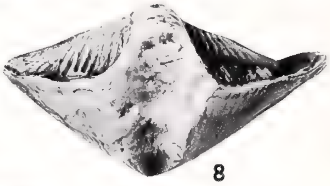
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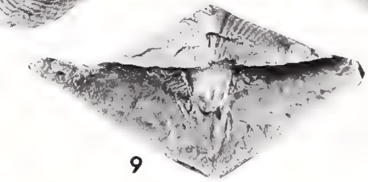
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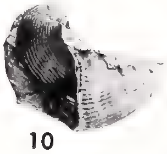
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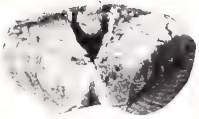
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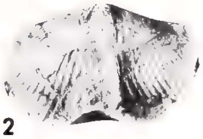
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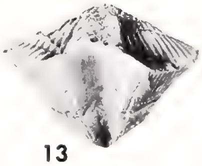
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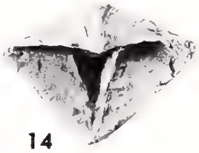
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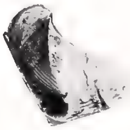
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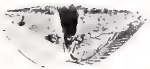
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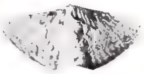
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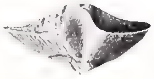
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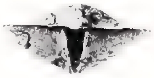
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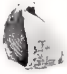
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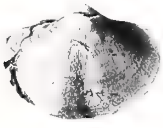
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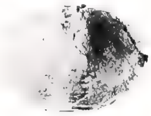
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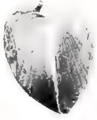
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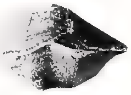
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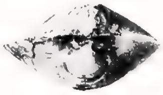
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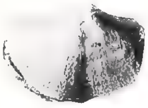
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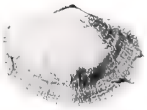
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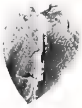
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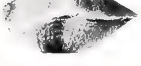
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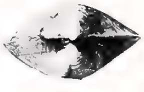
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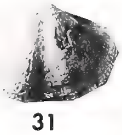
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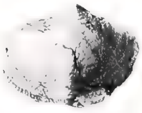
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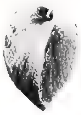
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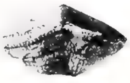
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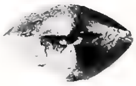
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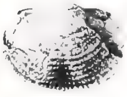
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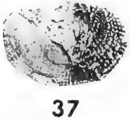
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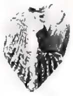
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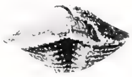
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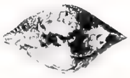
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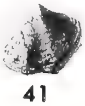
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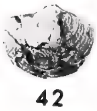
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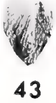
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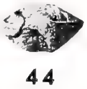
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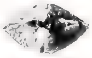
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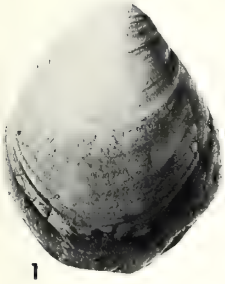
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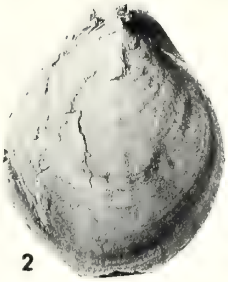
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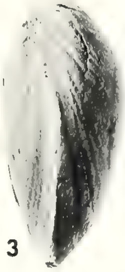
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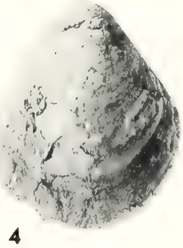
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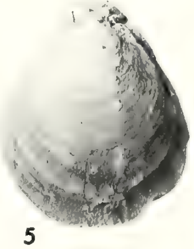
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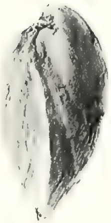
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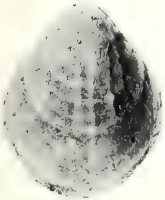
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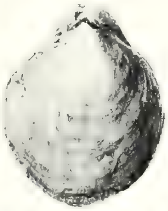
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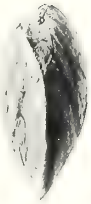
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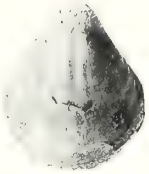
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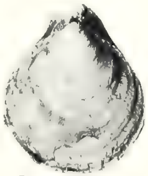
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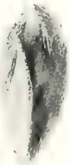
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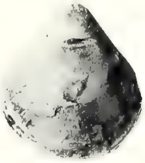
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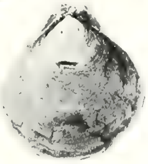
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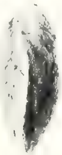
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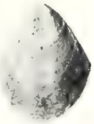
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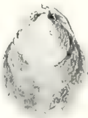
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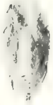
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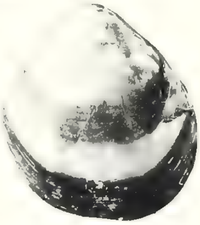
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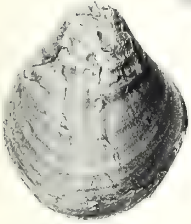
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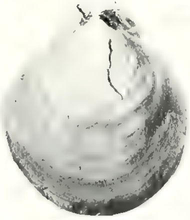
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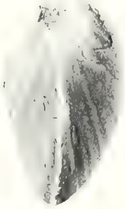
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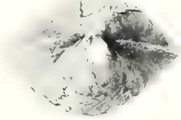
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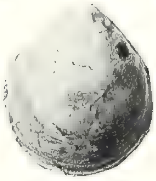
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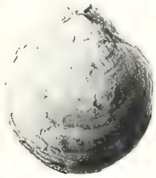
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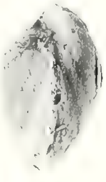
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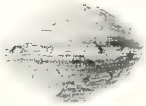
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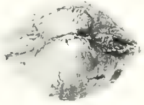
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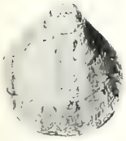
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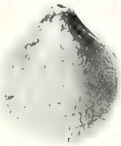
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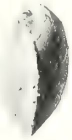
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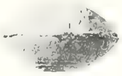
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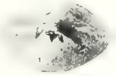
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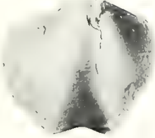
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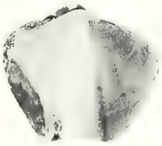
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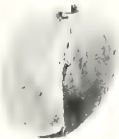
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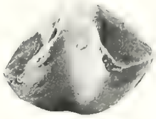
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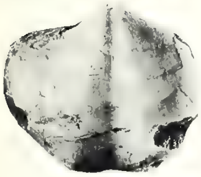
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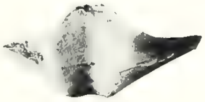
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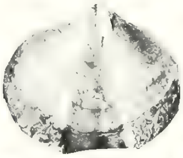
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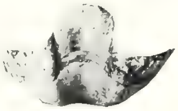
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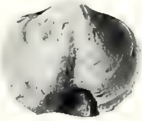
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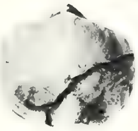
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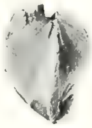
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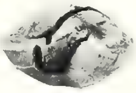
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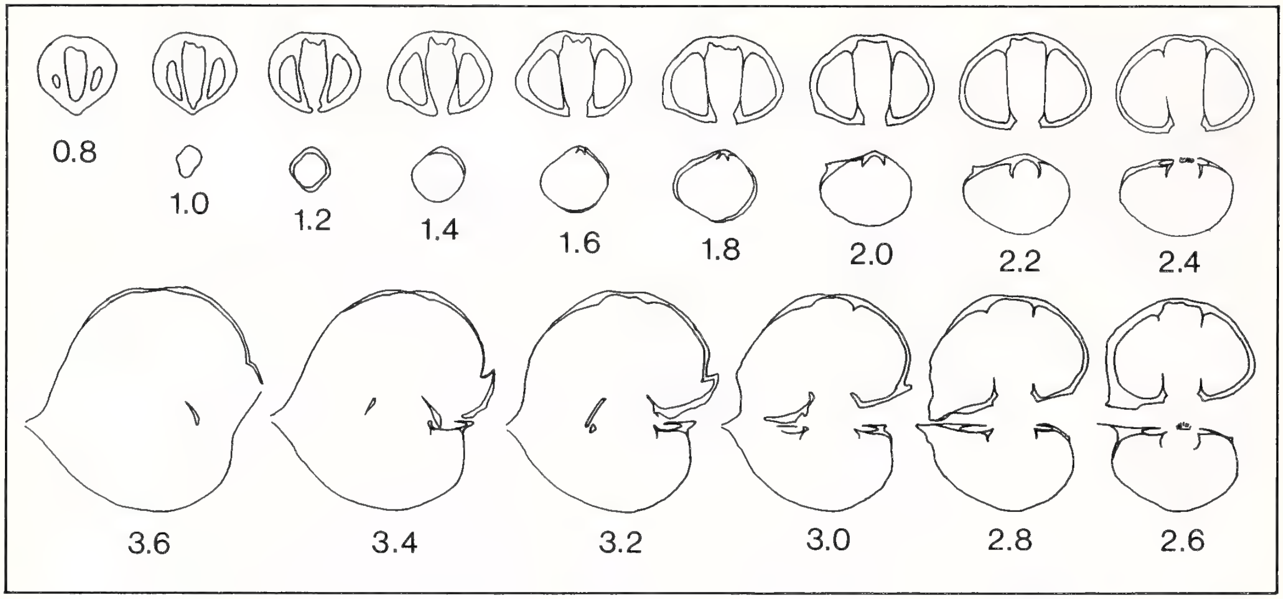


Fig. 25.—Transverse serial sections of *Eomartiniopsis kinderhookensis* n. sp. from SL392, CM 34742. Numbers refer to distance in mm from ventral beak. × 1.5.

Although this genus does not seem to bear septal plates, crural plates, tabellae, or similar structures, Fig. 149 shows a wide dorsally descending hingeplate which, with minor modification, could readily touch the floor of the valve. Johnson (1971:318) has shown that in at least some reticulariaceans the presence or absence of crural plates is not even of specific importance. For this reason, this new Glen Park species was assigned to *Eomartiniopsis* simply because the genus name has seniority.

Distribution.—The description given above is based on a single collection of 35 specimens, mostly disarticulated valves, from locality SL392. Two other valves come from locality SL394.

Order Spiriferinida Ivanova
Suborder Spiriferinidina Ivanova
Superfamily Syringothyridacea Frederiks
Family Syringothyrididae Frederiks
Subfamily Syringothyridinae Frederiks
Genus ***Syringothyris*** Winchell, 1863

Syringothyris extenuata (Hall, 1858)
Fig. 23.1–23.20

1858 *Spirifer extenuatus* Hall, p. 520, pl. 7, fig. 6.
1900 *Syringothyris extenuata* (Hall): Weller, p. 77–80, pl. 2, fig. 1–3, textfig. 1.
1914 *Syringothyris extenuata* (Hall): Weller, p. 386–388, pl. 72, fig. 5–12.

Holotype.—Whereabouts unknown.

Diagnosis.—Moderate sized to small *Syringothyris* with angular alate lateral extremities and a very short pedicle valve with a consistently strongly procline flattened ventral interarea.

Remarks.—This species presumably was described from a single brachial valve from the English River Sandstone at Burlington, Iowa. This specimen, the holotype, cannot be located by the present writer. Weller (1900, 1914) recollected and redescribed the species from English River Sandstone specimens and the present identification is based upon Weller's work. Weller (1900:78) clearly differentiated *Syringothyris extenuata* (Hall) from *Syringothyris halli* Winchell, 1863, which is from the superjacent McCraney Limestone, by its larger size, angular lateral extremities, and more procline interarea. The Glen Park Formation specimens illustrated here in Fig. 22 are all nearly complete but are crushed or have broken lateral extremities. This is a common species at most Glen Park localities and many pedicle valves are available for study. There is great variation in the height, flatness and inclination of the ventral interarea, much greater than Weller suggested, although the interarea is consistently procline.

Distribution.—This is a fairly common species at the following localities: SL392 (25 specimens), SL393 (36 specimens), SL396 (10 specimens), SL397 (8 specimens), SL511 (1 specimen).

Zeugopleura, new genus

Type species.—Spirifer jeffersonensis Weller, 1906, from the Glen Park Limestone at Glen Park Station, Jefferson County, Missouri (locality SL397).

Other species assigned.—Spirifer compositus Girty, 1928, from the Riddlesburg Shale Member of the Rockwell Formation, Bedford County, Pennsylvania.

Derivation of name.—From the Greek *zeugos*—pair, and *pleuron*—rib, referring to the pair of ribs in the ventral sulcus.

Stratigraphic range.—Early Kinderhookian.

Diagnosis.—Small to medium sized syringothyrididines with a pair of costae that rarely bifurcate in the ventral sulcus, moderately high concave procline ventral interarea, rounded lateral extremities, and a small apical subdelthyrial plate.

Description.—Small to medium size, transversely subelliptical in outline, unequally biconvex; pedicle valve subpyramidal with high slightly concave procline interarea and small slightly incurved beak; brachial valve moderately convex and similar to those of other syringothyrididines; ornament consisting of numerous simple rounded costae on flanks, two rarely bifurcating costae in the flattened sulcus, three or more on moderately flattened fold, and minute elongate papillae; ventral interior with small flattened apical subdelthyrial plate, syrinx lacking; dental adminicula slender, diverging, moderately long; dorsal interior spiriferoid with unsupported cardinalia; shell substance finely endopunctate.

Comparisons.—Zeugopleura n. gen. can best be compared with the following syringothyridine genera: *Pseudosyrinx* Weller, 1914, *Asyrinxia* Campbell, 1957, *Plicatosyrinx* Minato, 1952, and *Verkhotomia* Sokolskaya, 1963. *Pseudosyrinx* Weller differs from *Zeugopleura* n. gen. in having a smooth fold and sulcus and a large subdelthyrial plate. *Asyrinxia* Campbell can be differentiated by its alate lateral extremities, four to six weak obscure costae on the sides of the sulcus, and it lacks a subdelthyrial plate. *Plicatosyrinx* was described by Minato (1952:163) as externally having a ribbed fold and sulcus. Internally, it is said to possess a syrinx, but lacked dental plates and median septum, the shell substance being impunctate. *Verkhotomia* Sokolskaya is a much larger, strongly biconvex genus with a relatively low apsacline ventral interarea. It may have weak ribs on the sides of the sulcus but never has a pair on the floor of the sulcus. The perideltidial areas in *Verkhotomia plena* (Hall) are narrow, not wide as in *Zeugopleura jeffersonensis* (Weller).

Table 33.—*Measurements (in mm) of the illustrated specimens of* Zeugopleura jeffersonensis *(Weller, 1906) from the Glen Park Formation.*

Specimen no.	Locality	Length	Width	Thickness	Ribs/ flank
Pedicle valves					
Lectotype					
UC11350	SL397	17.8	22.4	10.1	10
IGS 80P84	SL393	17.9	27.8	11.8	11
IGS 80P85	SL393	17.5	27.8	11.2	12
CM 34743	SL396	16.3	27.0	9.5	12
IGS 80P86	SL393	14.4	24.2	10.0	12
IGS 80P87	SL393	11.9	14.4	6.1	8
IGS 80P88	SL393	10.3	15.3	6.5	9
Brachial valves					
IGS 80P89	SL393	16.5	28.5	7.4	10
CM 34744	SL396	16.0	27.3	6.4	11
CM 34745	SL396	13.3	22.4	5.1	10
Paralectotype					
UC11350	SL397	15.0	+20.9	+6.7	10
IGS 80P90	SL393	14.3	24.0	5.7	10
IGS 80P91	SL393	7.6	11.6	3.7	7
IGS 80P92	SL393	7.3	10.8	3.0	7

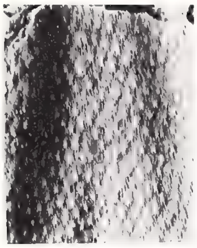
Zeugopleura jeffersonensis (Weller, 1906)
Fig. 26.1–26.39, 27

v*1906 *Spirifer jeffersonensis* Weller, p. 444–445, pl. 6, fig. 18–22.
1914 *Spirifer jeffersonensis* Weller: Weller, p. 369–370, pl. 42, fig. 17–21.
1938*a* *Spirifer jeffersonensis* Weller: Branson, p. 138, pl. 16, fig. 21, 22.

Lectotype.—Designated herein, a slightly smaller than average spalled pedicle valve, FMNH UC11350, Fig. 26.3–26.6, from Glen Park, Jefferson County, Missouri, SL397; illustrated by Weller (1906:pl. 6, fig. 19, 20; 1914, pl. 42, fig. 17, 18).

Paralectotypes.—Four spalled brachial valves, FMNH UC11350, one illustrated here as Fig. 26.36–26.37, same collection as the lectotype; three illustrated by Weller (1906:pl. 6, fig. 20–22; 1914:pl. 42, fig. 19–21); one small pedicle valve, FMNH UC11350, never illustrated, same collection as above.

Description.—Smaller than average for subfamily, unequally biconvex, transversely subelliptical in outline; lateral extremities well rounded in all growth stages, maximum width usually attained near or posterior to midlength; fold and sulcus well developed and defined, anterior commissure uniplicate; ornament consisting of from 10–12 simple rounded flattened costae on the flanks, two low, rounded costae that rarely bifurcate in the sulcus, three or more obscure costae on the fold, weak irregularly spaced growth varices, very faint closely and regularly spaced growth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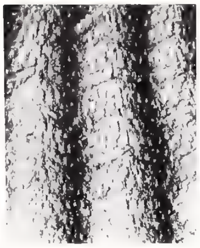
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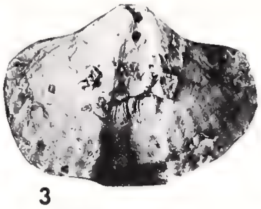
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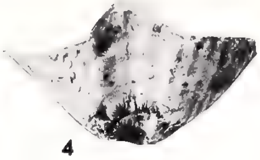
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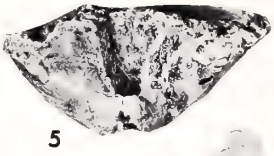
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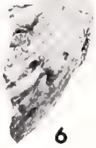
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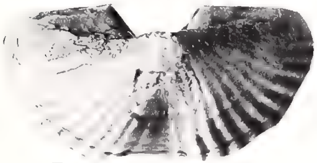
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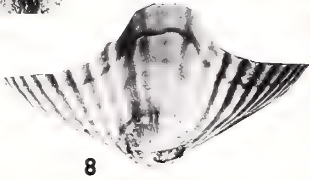
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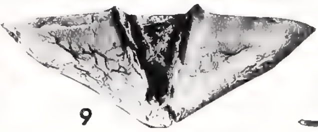
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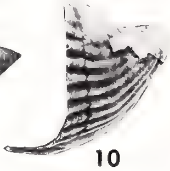
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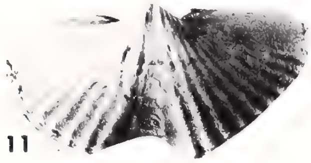
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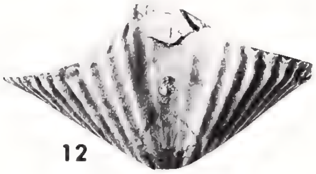
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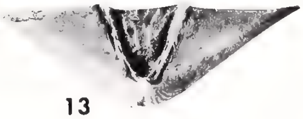
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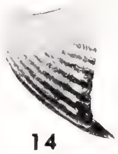
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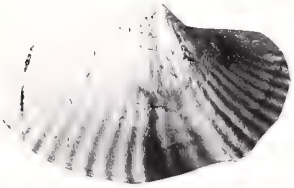
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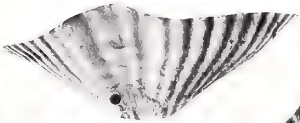
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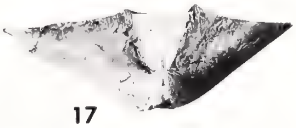
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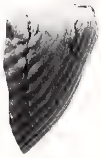
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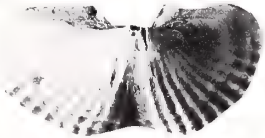
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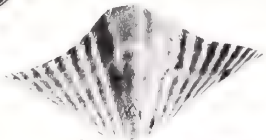
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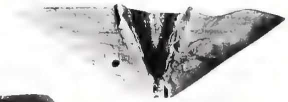
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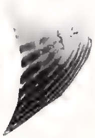
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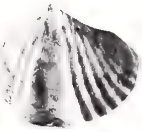
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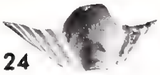
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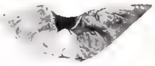
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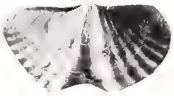
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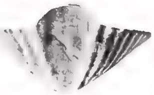
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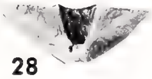
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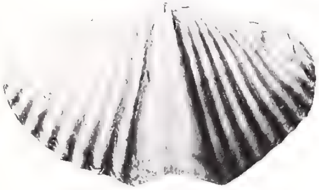
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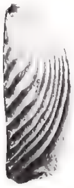
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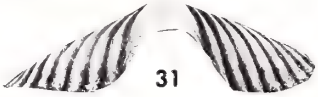
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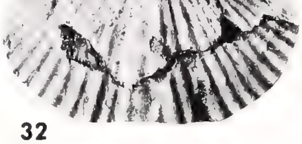
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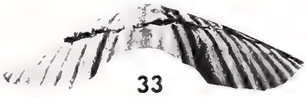
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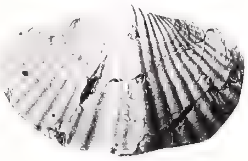
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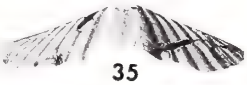
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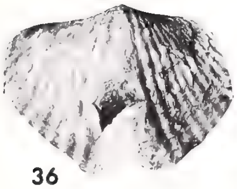
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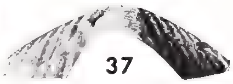
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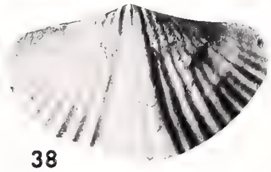
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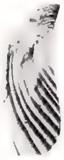
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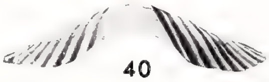
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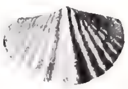
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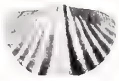
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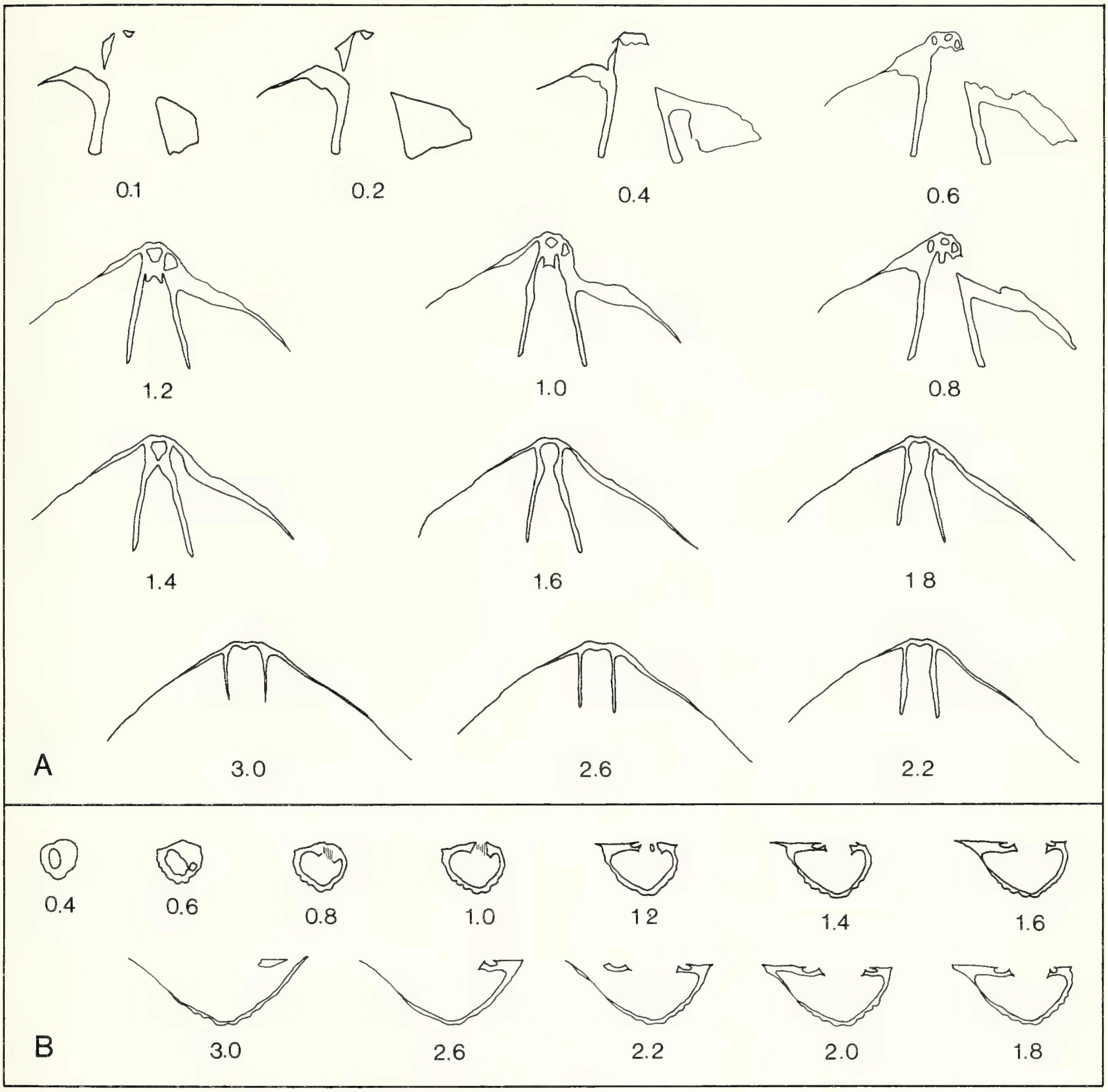

Fig. 27.—Transverse serial sections of *Zeugopleura jeffersonensis* (Weller) from SL397. A, large pedicle valve, CM 34746, ×1.5; B, medium sized brachial valve, CM 34747, ×2. Numbers refer to distance in mm from beak.

←

Fig. 26.—*Zeugopleura jeffersonensis* (Weller); 25.1, 25.2, micro-ornament (×10); 25.3–25.6, ventral, anterior, posterior and lateral views of the lectotype from SL397, FMNH UC11350; 25.7–25.14, 25.19–25.28, ventral, anterior, posterior and lateral views of five pedicle valves from SL393, IGS 80P84–80P88; 25.15–25.18, ventral, anterior, posterior and lateral views of an asymmetrical pedicle valve from SL396, CM 34743; 25.29–25.31, 25.38–25.40, dorsal, lateral and anterior views of two large spalled brachial valves from SL393, IGS 80P89, 80P90; 25.32–25.35, dorsal and anterior views of two large well preserved brachial valves from SL396, CM 34744, 34745; 25.36, 25.37, dorsal and anterior views of a brachial valve paralectotype from SL397, FMNH UC11350; 25.41, 25.42, two small brachial valves from SL393, IGS 80P91, 80P92; all ×1.5 except 25.1 and 25.2, ×10.

lines, and slightly coarser elongated papillae arranged in quincunx; shell substance finely endopunctate.

Pedicle valve subpyramidal, much thicker than brachial valve, with maximum thickness in umbonal region; flanks sloping evenly to antero-lateral margins; umbonal region strongly inflated with small acute incurved beak; ventral interarea procline, or more rarely, nearly catacline, high, weakly concave, defined by slightly rounded beak ridges; longitudinally grooved perideltidial areas large, extending over most of interarea; delthyrium moderately broad but higher than wide; subdelthyrial plate small, set well below surface of interarea between dental adminicula; deltidial cover not observed; sulcus originating at beak as narrow groove, becoming deeper and wider anteriorly but remaining shallow throughout with flattened bottom in most specimens, rarely rounded, producing moderate tongue; interior with long diverging dental adminicula that extend forward one-third to one-half length of valve.

Brachial valve transversely subelliptical in outline, most convex in umbonal region, and much thinner than opposite valve with maximum thickness near or posterior to midlength; umbo slightly swollen; flanks sloping evenly to antero-lateral margins, more steeply toward hingeline; fold originating at small inconspicuous dorsal beak, well defined by sulcus-bounding grooves, rising moderately toward anterior margin, often becoming slightly flattened medially; interior with unsupported striate cardinal process and wide sockets; other internal details not observed.

Distinguishing characters.—This species is characterized by its transversely subelliptical outline, moderately high concave procline ventral interarea with large perideltidial areas, well-defined low fold and shallow flattened sulcus with a pair of ribs in the sulcus, and 10–12 simple flattened costae on the flanks.

Remarks.—*Zeugopleura jeffersonensis* (Weller) is not readily confused with other syringothyrididines in the North American mid-continent. *Spirifer compositus* Girty, 1928, from the Riddlesburg Shale of Pennsylvania is closely similar to the Glen Park species. It differs, if at all, in its smaller size and better defined ribs in the sulcus and on the fold. Girty (1928:118) stated that no subdelthyrial plate was present but his specimens were distorted molds and fragments and clearly did not afford a complete description of the species.

Distribution.—*Zeugopleura jeffersonensis* (Weller) is one of the most common Glen Park species, occurring in abundance at localities SL393, SL396, and SL397. It is less common at localities SL395 (1 specimen) and SL511 (7 specimens).

Order Terebratulida Waagen
Suborder Terebratulidina Waagen
Superfamily Dielasmatacea Schuchert
Family Cranaenidae Cloud
Subfamily Cranaeninae Cloud
Genus ***Hamburgia*** Weller, 1911

Hamburgia typa Weller, 1911
Fig. 24.1–24.34, 28

v*1911 *Hamburgia typa* Weller, p. 446, fig. 6.
v*1914 *Hamburgia typa* Weller: Weller, p. 283–284, pl. 31, fig. 16–18; textfig. 36.

Lectotype.—Designated herein, a medium sized pedicle valve, FMNH UC14245, Fig. 24.19, Weller Collection, from locality SL395, Hamburg, Calhoun County, Illinois; illustrated by Weller (1914:pl. 31, fig. 16).

Paralectotypes.—19 in all, all numbered FMNH UC14245; one pedicle valve and one brachial valve were illustrated by Weller (1914:pl. 31, fig. 17, 18); same collection as the lectotype.

Emended description.—Average size for genus, subequally biconvex, outline usually almost symmetrical, longitudinally subelliptical, subrhomboidal or obscurely subpentagonal; greatest width near midlength; lateral profile lenticular; greatest thickness slightly posterior to midlength; anterior commissure rectimarginate; fold and sulcus lacking; ornamentation lacking except for concentric color banding on lectotype (see Fig. 24.19) and irregularly spaced growth lines.

Pedicle valve moderately and evenly convex, most convex in umbonal region; venter rounded, flanks sloping evenly to antero-lateral margins, more steeply to cardinal margins; umbonal region narrowly swollen, beak suberect, foramen large, ovate, labiate, permesothyridid or epithyridid; beak ridges rounded, poorly defined; delthyrium closed by conjunct deltidial plates; interior with short pedicle collar, slender diverging dental plates that closely approximate sides of umbonal region, and bladelike teeth.

Brachial valve most convex umbonally, evenly convex on dorsum, flanks sloping gently and evenly to antero-lateral margins; umbonal region defined by concave flexures, lateral extremities slightly compressed; beak small, obscured by ventral beak; interior with open umbonal region; sockets broad and deep, inner socket ridges stout and high; deeply concave hingeplate sessile posteriorly, rising slightly off floor of valve anteriorly; crural bases originate anteriorly at free end of hingeplate as V-shaped processes; crural processes very high, nearly parallel, extending into ventral valve in juveniles (Fig. 28B); loop short, with narrow ventrally convex transverse band in adults and short vertical medial plate in juveniles.

Distinguishing characters.—The nearly symmetrical subrhomboidal to subelliptical outline, moderate size, and weakly convex flanks serve to characterize this species.

Remarks.—*Hamburgia chappelensis* Carter, 1967, from the Chappel Limestone of central Texas and *Hamburgia flora* (Winchell) from the Logan Formation of Ohio as illustrated by Hyde (1953:pl. 37, fig. 1–12, 17–20) can both be distinguished from *Hamburgia typa* Weller by their larger size and subpentagonal outlines. One of Hyde's drawings (1953: pl. 37, fig. 19) shows very high crural processes, extending into the cavity of the pedicle valve, which

Table 34.—*Measurements (in mm) of the lectotype and three mature complete specimens of* Hamburgia typa *Weller, 1911, from the Glen Park Formation.*

Specimen no.	Locality	Length	Width	Thickness
Lectotype (pedicle valve)				
FMNH UC14245	SL395	19.8	18.2	8.1
CM 34734	SL393	20.0	16.9	11.2
CM 34735	SL393	15.7	13.4	9.2
CM 34736	SL393	12.5	11.4	6.7

suggests that unusually high crural processes may be of taxonomic importance in the definition of this genus.

Distribution.—This is a common species at localities SL393, SL395 and SL396.

Family Heterelasminidae Likharev
Genus *Beecheria* Hall and Clarke, 1893

Beecheria paraplicata Rodriguez and Gutschick, 1967
Fig. 29.31–29.43

1967 *Beecheria paraplicata* Rodriguez and Gutschick, p. 381, pl. 44, fig. 1–5, 30, 39, 40.

Holotype.—UND 354, from Unit E of the Sappington Formation, western Montana. The authors considered this unit to be of Mississippian age but Sando et al. (1969:E9) suggested that this unit is Devonian.

Paratypes.—UND 335, UND 356–360.

Diagnosis.—Large *Beecheria* with subtruncate anterior margin and paraplicate anterior commissure.

Remarks.—The dorsal sulcus in these Glen Park specimens is not quite as distinct as in the Sappington types. These Glen Park specimens are moderately smaller than the Sappington specimens measured by Rodriguez and Gutschick (1967:table 4) but otherwise agree in most respects with their description of *Beecheria paraplicata.* The specimens illustrated here show the range of variation in size and proportions of typical Glen Park specimens. Most specimens are wider than Fig. 29.31 and narrower than Fig. 29.39.

Table 35.—*Measurements (in mm) of the illustrated specimens of* Beecheria paraplicata *Rodriguez and Gutschick from the Glen Park Formation at locality SL393, Pike County, Illinois.*

Specimen no.	Length	Width	Thickness
Pedicle valves			
IGS 80P100	32.8	21.7	12.5
IGS 80P101	25.7	18.5	9.0
IGS 80P102	22.0	17.5	5.5
Brachial valves			
CM 34748	27.2	23.3	6.5
IGS 80P103	24.9	22.9	6.6
IGS 80P104	29.0	22.1	8.1

Rodriguez and Gutschick compared juveniles of their new species with *Beecheria chouteauensis* (Weller, 1914). Mature specimens are readily distinguished by their paraplicate anterior commissure.

Distribution.—In the Glen Park Formation this species is common at locality SL393 (23 specimens), and rare at SL396 (1 specimen), and SL397 (9 specimens).

Superfamily Cryptonellacea Thomson
Family Cryptonellidae Thomson
Genus *Dielasmella* Weller, 1911

Dielasmella compressa (Weller, 1906)
Fig. 29.1–29.30, 30

v*1906 *Eunella compressa* Weller, p. 442–443, pl. 6, fig. 13–16.

1911 *Dielasmella compressa* (Weller): Weller, p. 447, fig. 7a–f.

1914 *Dielasmella compressa* (Weller): Weller, p. 280–281, pl. 30, fig. 43–55.

v.1914 *Dielasmella calhounensis* Weller, p. 281–282, pl. 31, fig. 1–4, textfig. 35.

1938*a* *Dielasmella compressa* (Weller): Branson, p. 134, pl. 16, fig. 16–18.

?1938*b* *Dielasmella compressa* (Weller): Branson, p. 31, pl. 22, fig. 23, 24.

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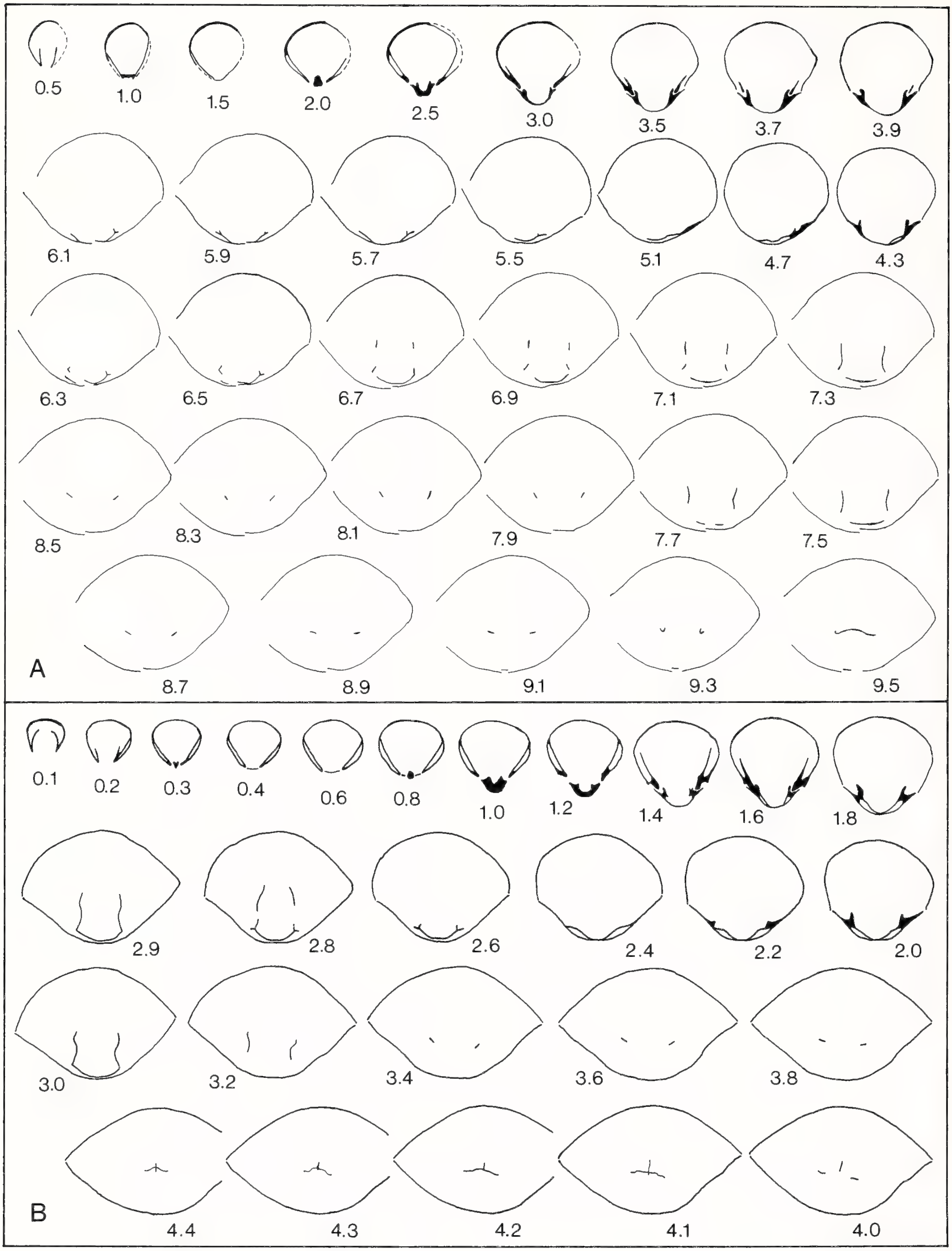
Fig. 28.—Transverse serial sections of *Hamburgia typa* Weller from SL397. A, large specimen with fractured dorsum, IGS 80P93, ×2; B, small immature specimen, IGS 80P94, ×5. Numbers refer to distance in mm from beak.

Fig. 29.—Terebratulids. 29.1–29.30, *Dielasmella compressa* (Weller); 29.1–29.6, ventral, dorsal and lateral views of two large specimens from SL395, syntypes of *Dielasmella calhounensis* Weller, FMNH UC14246; 29.7–29.21, ventral, dorsal and lateral views of five medium sized specimens from SL393, IGS 80P95–80P99; 29.22–29.30, ventral, dorsal and lateral views of three small specimens from the Weller Collection, SL397, paralectotypes FMNH UC11347; all ×3. 29.31–29.43, *Beecheria paraplicata* Rodriguez and Gutschick; 29.31–29.36, ventral and lateral views of three pedicle valves, IGS 80P100–80P102; 29.37–29.43, dorsal and anterior views of three brachial valves, CM 34748 and IGS 80P103, 80P104, respectively, all from SL393; all ×1.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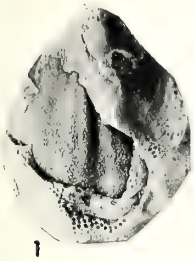
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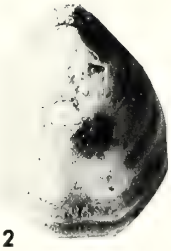
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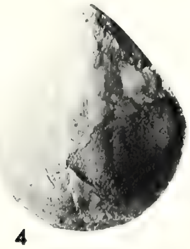
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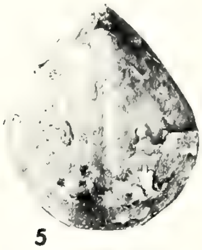
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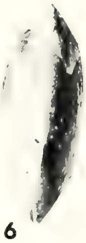
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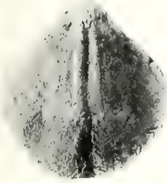
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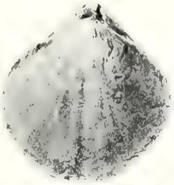
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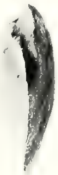
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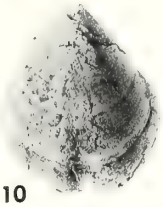
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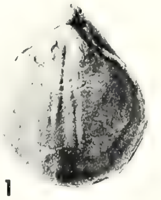
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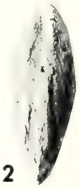
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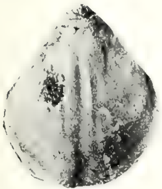
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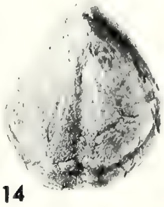
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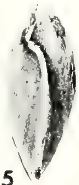
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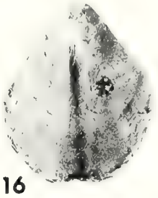
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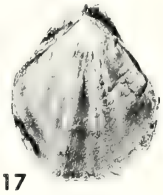
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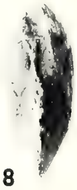
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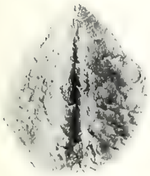
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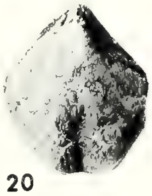
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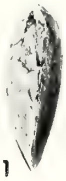
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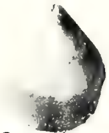
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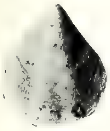
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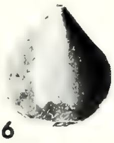
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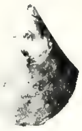
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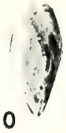
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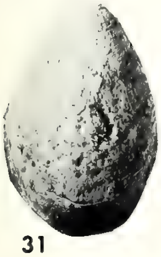
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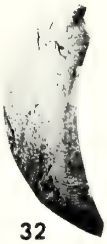
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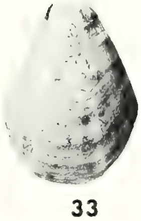
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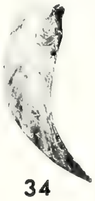
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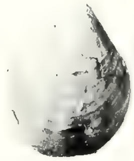
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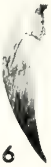
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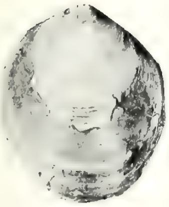
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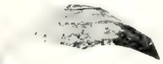
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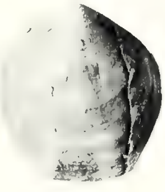
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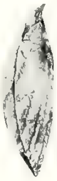
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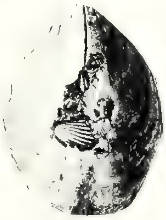
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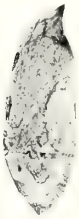
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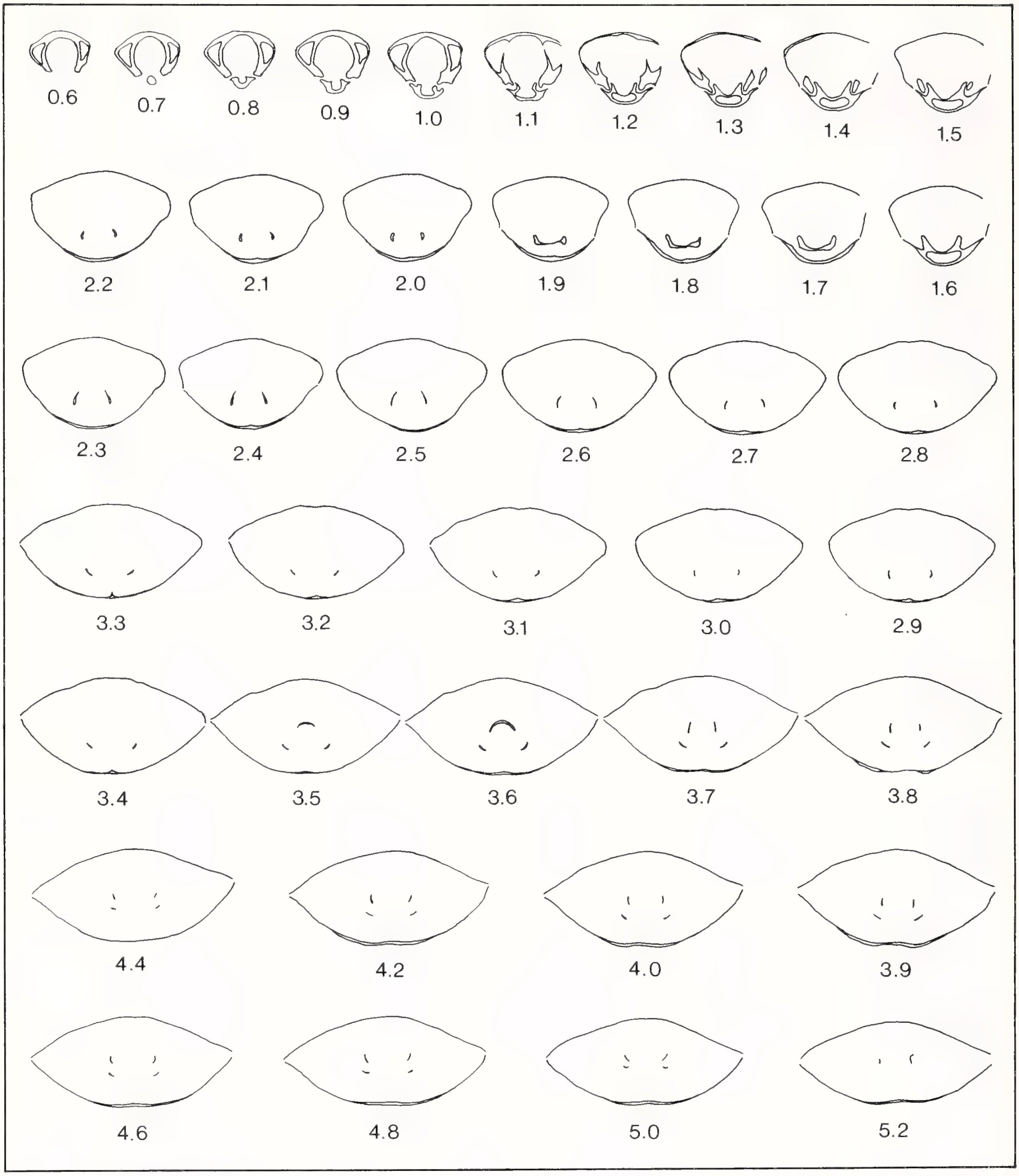

Fig. 30.—Transverse serial sections of a medium sized *Dielasmella compressa* (Weller) from SL393, IGS 80P105. Numbers refer to distance in mm from ventral beak. ×4.

1938*a* *Dielasmella calhounensis* Weller: Branson, p. 170, pl. 19, fig. 26, 27.
1944 *Dielasmella calhounensis* Weller: Cooper, p. 364, pl. 143, fig. 14–15.
1962 *Dielasmella compressa* (Weller): Stehli, p. 102, pl. 20, Group K.
1965 *Dielasmella compressa* (Weller): Stehli, p. 762, fig. 621: 4a, 4b.

Lectotype.—Designated herein, FMNH UC11347, Weller Collection from Glen Park, Missouri; illustrated by Weller (1906:pl. 6, fig. 13 and 1914:pl. 30, fig. 47, 48, 54, 55); not reillustrated here. Of Weller's four illustrated syntypes this small specimen most closely approaches the outline of larger more typical specimens within the syntype suite as well as from other localities.

Paralectotypes.—Fourteen in all, FMNH UC11347, same collection as the lectotype. Weller illustrated three of these specimens (1906:pl. 6, fig. 14–16; 1914:pl. 30, fig. 43–46, 49–53). Three additional syntypes of more typical outline are illustrated here for the first time on Fig. 29.22–29.30.

Diagnosis.—Small, thin, elongate *Dielasmella* with long umbonal region, straight to weakly concave posterolateral margins with sharp subangular beak ridges, and guttate to subrhomboidal outline; flanks flattened and smooth; greatest width anterior to midlength; weak narrow sulcus often present in one or both valves producing truncated or emarginate outline in those specimens.

Remarks.—I have placed the larger of Weller's two *Dielasmella* species, *Dielasmella calhounensis* Weller, 1914, in synonomy with *Dielasmella compressa* (Weller, 1906). Weller (1914:282) expressed doubt about the validity of *Dielasmella calhounensis* when he proposed it, noting that

> . . . it is always a larger form, however, with the brachial valve relatively more convex and with the median sinus of the pedicle valve more conspicuously developed.

On Fig. 29 the lateral profile of Weller's types of *Dielasmella calhounensis* Weller and eight smaller specimens readily assignable to *Dielasmella compressa* (Weller) can be compared for relative convexity of the valves. It can be seen at once that there is little difference between the two groups of figures. The degree of development of the ventral sinus can also be seen to be similar in both groups of figures. After examining many specimens assignable to both taxa, I can find no validity to Weller's contention that the ventral sinus is better developed in *Dielasmella calhounensis.* In Table 36, the specimens from locality SL393 show size range overlap between the types of *Dielasmella compressa* (Weller) on the one hand and the types of *Dielasmella calhounensis* Weller on the other. It should be reiterated here that specimens of several Glen Park species that occur in both Missouri and Illinois are generally smaller in Missouri than they are in Illinois. These include *Tylothyris missouriensis* (Weller), *Plicochonetes? glenparkensis* (Weller), *Nucleospira minima* Weller, and *Dielasmella compressa* (Weller).

Table 36.—*Measurements (in mm) of* Dielasmella compressa *(Weller, 1906) from the Glen Park Formation. Specimens marked with an asterisk * are illustrated on Fig. 28. Those marked with a dagger † were illustrated by Weller (1914).*

Specimen no.	Locality	Length	Width	Thickness
FMNH UC11347	SL397	3.9	3.1	1.6
FMNH UC11347	SL397	4.3	3.3	1.6
FMNH UC11347	SL397	4.6	3.8	1.7
FMNH UC11347	SL397	4.7	4.2	1.8
FMNH UC11347*	SL397	5.4	4.7	2.4
FMNH UC11347*	SL397	5.5	4.9	2.1
FMNH UC11347†	SL397	5.6	4.3	2.0
Lectotype†	SL397	5.9	5.0	2.0
FMNH UC11347*	SL397	6.0	5.0	2.2
FMNH UC11347†	SL397	+6.3	6.6	2.6
FMNH UC11347†	SL397	6.4	6.1	2.4
IGS 80P99	SL393	5.6	4.7	2.1
IGS 80P98	SL393	6.0	4.4	1.7
IGS 80P97	SL393	6.5	5.6	2.5
IGS 80P95	SL393	6.7	6.1	2.5
IGS 80P96	SL393	7.0	5.3	2.4
IGS 80P106	SL393	7.5	5.6	2.7
IGS 80P107	SL393	7.7	6.7	2.7
IGS 80P108	SL393	8.2	6.7	3.1
IGS 80P109	SL393	8.2	7.7	3.0
IGS 80P110	SL393	8.3	6.9	3.2
IGS 80P111	SL393	8.7	7.2	2.9
CM 34751	SL396	10.1	8.1	—
FMNH UC14246	SL395	8.8	7.9	—
FMNH UC14246†	SL395	10.0	8.6	3.8
FMNH UC14246†	SL395	10.7	8.6	4.5
FMNH UC14246	SL395	11.7	10.5	—
FMNH UC14246	SL395	11.8	11.3	—
FMNH UC14246	SL395	12.3	10.7	—

The only other North American species assigned to this genus is *Dielasmella larga* Carter, 1967, from the Chappel Limestone of central Texas. The latter is larger, much thicker, with weak lateral ribs on the flanks, and the maximum width is attained posteriorly, not anteriorly as in *Dielasmella compressa* (Weller).

Figure 30 shows detailed serial sections of the interior of *Dielasmella compressa* (Weller) from Brown Branch, Pike County, Illinois. These sections are in general agreement with those of Weller (1911) for *Dielasmella compressa* from Glen Park, Missouri, and Stehli's (1962) photographs of the loop of a specimen from the Hamburg Oolite at Hamburg, Illinois. One minor difference is that the transverse band in the Pike County specimen is posteriorly convex similar to most dielasmataceans, not weakly concave as indicated by Stehli (1962:text-fig. 1C).

Distribution.—This species is moderately common at localities SL397 (more than 22 complete specimens, plus disarticulated valves), SL393 (25 complete specimens, numerous disarticulated valves), and SL395 (2 complete specimens, 9 disarticulated valves, numerous specimens in other museums). One large specimen was recovered at locality SL396.

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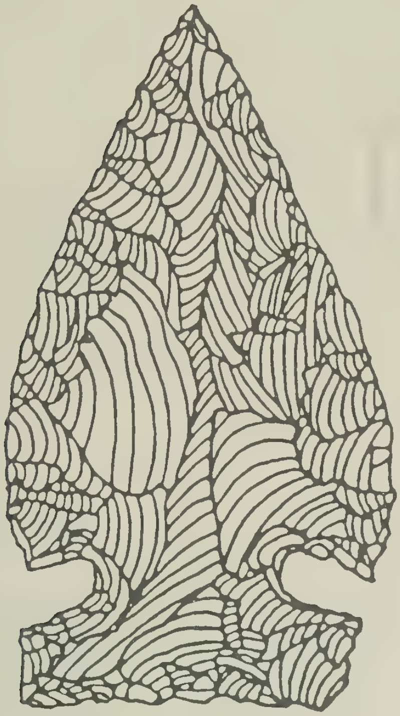

AGE, DISTRIBUTION AND CULTURAL AFFILIATION OF RACCOON NOTCHED POINT VARIETIES IN WESTERN PENNSYLVANIA AND WESTERN NEW YORK

STANLEY W. LANTZ
Staff Archaeologist, Division of Anthropology

Edited by VERNA L. COWIN
Assistant Curator, Division of Anthropology

NUMBER 28

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ABSTRACT

Raccoon Notched point types and associated tools of the Raccoon Notched Point Assemblage are fully described, illustrated, and subjected to analyses of age, geographic distribution, and lithic source material.

Large centrally located Middle Woodland Raccoon Notched point sites in western Pennsylvania and western New York are classified as Regional Centers and these centers and their ancillary sites, including burial mounds, are discussed and plotted on maps.

Regional differences are examined and descriptions of selected Middle Woodland point types from these areas are presented. Illustrations are provided for the Bennington Corner Notched, Garvers Ferry Corner Notched, Kiski Notched, and Murphys Stemmed points.

A new Middle Woodland phase is defined for the study area. The Allegheny River phase, and its associated Raccoon Notched Point Assemblage, are dated at A.D. 500 to A.D.950. Extensive appendices are included in support of the conclusions.

INTRODUCTION

In 1941 Edmund S. Carpenter, under sponsorship of the Pennsylvania Historical and Museum Commission, initiated a research project to explore burial mound locations in the upper Allegheny Valley. Carpenter excavated a number of mound structures and reported the results of both his work and prior mound investigations in western Pennsylvania. His original manuscript, "Ancient Mounds of Pennsylvania," is housed at the American Philosophical Society Library in Philadelphia and sections of the manuscript were published in *The Pennsylvania Archaeologist* (Carpenter, 1956).

Then, in 1950, The Carnegie Museum of Natural History (CMNH) initiated systematic archaeological surveys in the upper Ohio drainage and this research interest continues to the present. Initially the project was directed by James L. Swauger, and the first fieldwork was conducted by William J. Mayer-Oakes, who published the results in 1955 as *The Prehistory of the Upper Ohio Valley.* Ten years later, William A. Ritchie published *The Archaeology of New York State,* which included an important Middle Woodland chronology for his central and western New York subareas.

More than two decades have passed since Ritchie's memorable work, yet few new excavations have been reported and no major publications have addressed Middle Woodland manifestations in western New York and western Pennsylvania. To fill this gap, an intensive survey of the site-recording files housed at the Division of Anthropology at CMNH was launched, the Division's field associates and regional representatives were consulted, and Middle Woodland artifacts in private collections throughout the study area were documented. The primary goal of the research project was to add to the data base established by Carpenter, Mayer-Oakes, and Ritchie. This is accomplished herein by fully describing and dating Raccoon Notched projectile point types and associated tools and identifying a Raccoon Notched Point Assemblage. Five basic point types, four knife forms, four drills, as well as strike-a-lights and scrapers, are illustrated. Suggested dates for the assemblage are A.D. 500 to A.D. 950, and available illustrations of associated ceramics and ground stone tools are included.

When plotting the areal distribution of this newly defined assemblage, it became apparent that at least seven major occupational loci were associated with numerous smaller sites. It is hypothesized that these major occupation zones served as "Regional Centers" during the Middle Woodland period. The centers, their ancillary sites, and the locations of known burial mounds are described and illustrated.

The final sections of this report address regional differences. In all areas, triangular points are noted as associated with Raccoon Notched points. Regional studies align the Raccoon Notched materials from southwestern Pennsylvania with the previously hypothesized Watson tradition of West Virginia (Hemmings, 1984:47; Maslowski, 1985:30) and the recently typed Bennington Point (Fogelman, 1984; Boldurian, 1985:171, 172).

In west central Pennsylvania, Raccoon Notched points and possibly the recently typed Garvers Ferry Corner Notched, Kiski Notched, and Murphys Stemmed points (George, 1982:181–209) appear to be associated with the southern Ohio Intrusive Mound Culture (Morgan, 1952:83–98). Other shared traits include Mahoning Ware ceramics, keeled-base platform pipes, and pendants. Here a continuous Middle Woodland connection with Ohio is documented by the presence of high percentages of Upper Mercer and Vanport lithics.

Based on preliminary findings, the Allegheny River phase, a new Middle Woodland manifestation associated with the utilization of Raccoon Notched tools, is proposed. This phase is evident in the upper Allegheny valley from Warren, Pennsylvania, upriver to Olean, New York, and northwest toward Lake Erie. It must be emphasized that some of the assignations to known traditions and to a newly assigned phase are tentative concepts and, in some cases, lack sufficient supporting data. Nonetheless, the data at hand can be used to construct a Middle Woodland chronology for the Upper Ohio Valley.

THE RACCOON NOTCHED POINT ASSEMBLAGE

Background

Although the Raccoon Notched point has appeared in the literature since 1955 and is referred to by professional and non-professional archaeologists as a specific type in western Pennsylvania, New York, and Ohio, it has never been fully described in its various forms (Cowin, 1980:21; Eisert, 1981:28, 29; George, 1975:26–28; George and Bassinger, 1975:14, 15; Johnson, et al., 1979:73; Lantz, 1975:11; Prufer, 1967*a,* 1967*b*:22, 285, 292, 300, 303, 305; Seeman, 1980:11). Metric measurements and size ranges have not been fully published; nor have all the major sites producing these points been reported.

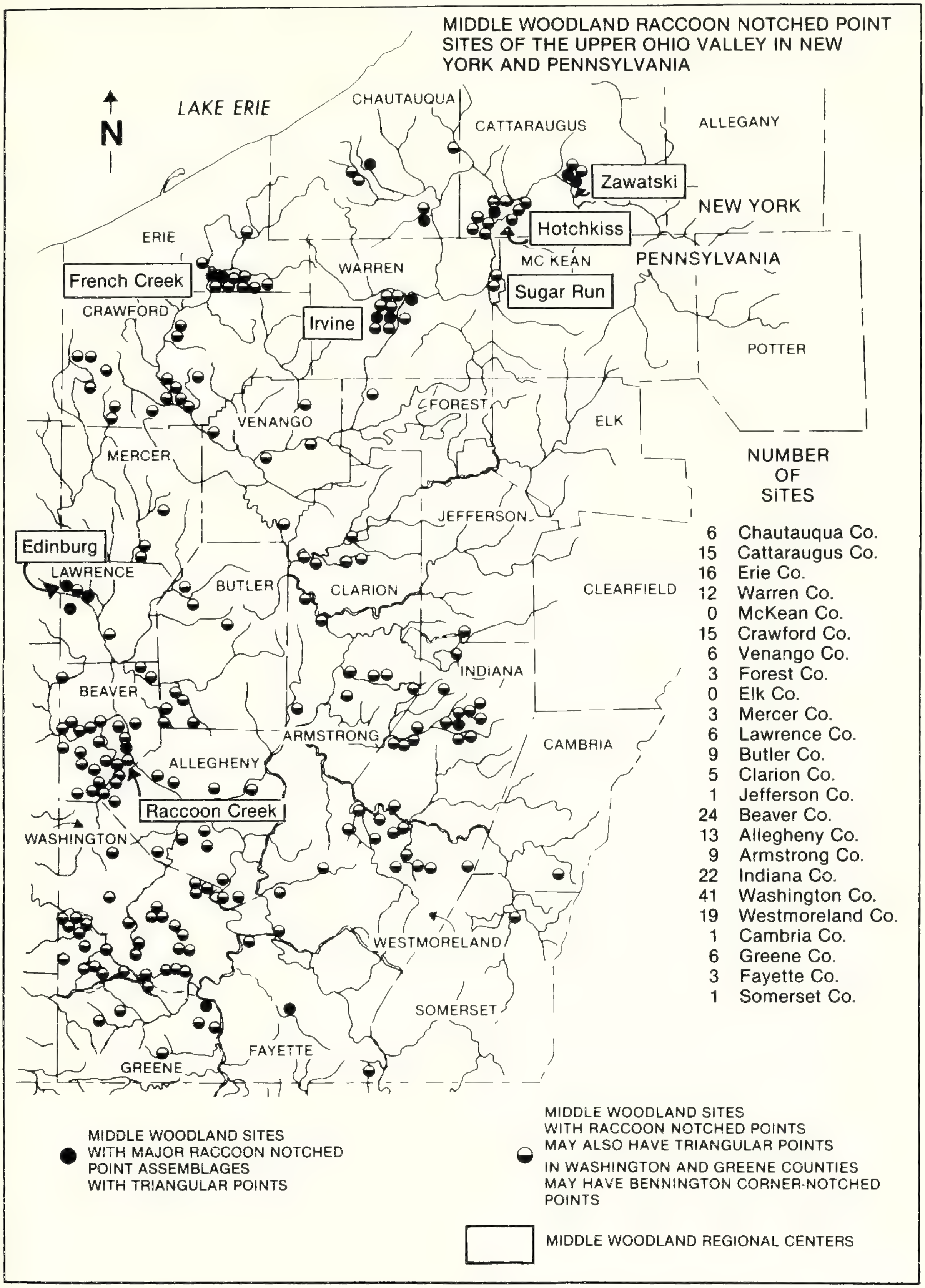
Raccoon Notched points and associated tool forms were first recognized by Emil Alam and Vincent Mrozoski. Beginning in the late 1930s, Alam systematically conducted an archaeological survey along southwestern Pennsylvania's Raccoon Creek and acquired a large collection of points and other artifacts which he subsequently donated to the Division of Anthropology at CMNH. Alam collected a quantity of Raccoon Notched points from the Outdoor Theater site (36 BV 24) which he designated the type site (Alam, 1972:4). When Alam and Mrozoski brought the distinctive points to the attention of the Museum in 1952, William J. Mayer-Oakes, recognizing that this point was prevalent in the Upper Ohio Valley, established the typology by describing the side- and corner-notched points as well as some of the base and blade characteristics (Mayer-Oakes, 1955). Later Alam described the side-notched variety, a drill, and two preforms (Alam, 1972:4).

Ritchie refers to the Raccoon Notched points as being similar to points found with a Kipp Island phase child burial excavated at Port Maitland, Welland County, Ontario (Ritchie, 1965:231; Plate 81). He tentatively typed two thin, well-made, side-notched, New York points as Long Bay and Maitland points (Ritchie, 1965:203–213; 1971:125). These points, especially the Maitland, resemble the Raccoon Notched points so closely that Mayer-Oakes included the Maitland point as one of the side-notched varieties of the Raccoon Notched point type (Mayer-Oakes, 1955:86, Plate 34). However, Ritchie's types cannot be fully compared to the Raccoon point types described in this report because metric data are not available for either the Long Bay or the Maitland points (Ritchie, 1971:125).

In 1947 and 1951, Ritchie excavated thin, corner-notched points at the Jack's Reef site, Onondaga County, New York, and typed them as Jack's Reef Corner Notched points (Ritchie, 1971:26–27). He lists the length range of these points as generally between 4.5 to 5 cm in length (Ritchie, 1971:26). In contrast, the majority of the corner-notched varieties of the Raccoon Notched point are from 3 to 4.3 cm, averaging 3.3 cm.

Similar points have also been typed in other states, but some of these are considered to be later than the dated western Pennsylvania Raccoon Notched types. These include the Late Woodland "Corner Notched Woodland" point of Alabama and the Knight Island point reported from Tennessee (Cambron and Hulse, 1969:69, 71). Also similar is the Reed point from Oklahoma, considered to be related to both the Gibson aspect of Middle Woodland and the Fulton aspect of Late Woodland (Bell, 1958). The pentagonal corner-notched Intrusive Mound points of Ohio (Converse, 1973:63) are comparable to Type 4 in this report's typology. Waldorf and Waldorf (1987:195) describe the Intrusive Mound point as almost identical to the New York Jack's Reef point; however, lengths of the Intrusive Mound points range from 3.8 to 4.4 cm, longer than either the Jack's Reef or the Raccoon Notched forms.

When Mayer-Oakes established his basic typology in 1952, he noted the presence of Raccoon Notched points along the Mahoning and Beaver drainages in Lawrence County and at Raccoon Creek in Beaver County, Pennsylvania. Examination of the Alam collection confirmed the presence of these distinctive points in the upper French Creek drain-


MIDDLE WOODLAND RACCOON NOTCHED POINT SITES OF THE UPPER OHIO VALLEY IN NEW YORK AND PENNSYLVANIA
N
LAKE ERIE
CHAUTAUQUA
CATTARAUGUS
ALLEGANY
Zawatski
NEW YORK
Hotchkiss
PENNSYLVANIA
ERIE
MC KEAN
French Creek
WARREN
Sugar Run
CRAWFORD
Irvine
POTTER
FOREST
VENANGO
ELK
MERCER
JEFFERSON
Edinburg
LAWRENCE
BUTLER
CLARION
CLEARFIELD
INDIANA
BEAVER
ARMSTRONG
CAMBRIA
ALLEGHENY
Raccoon Creek
WASHINGTON
WESTMORELAND
SOMERSET
FAYETTE
GREENE
● MIDDLE WOODLAND SITES WITH MAJOR RACCOON NOTCHED POINT ASSEMBLAGES WITH TRIANGULAR POINTS
◒ MIDDLE WOODLAND SITES WITH RACCOON NOTCHED POINTS MAY ALSO HAVE TRIANGULAR POINTS IN WASHINGTON AND GREENE COUNTIES MAY HAVE BENNINGTON CORNER-NOTCHED POINTS
☐ MIDDLE WOODLAND REGIONAL CENTERS

NUMBER OF SITES	
6	Chautauqua Co.
15	Cattaraugus Co.
16	Erie Co.
12	Warren Co.
0	McKean Co.
15	Crawford Co.
6	Venango Co.
3	Forest Co.
0	Elk Co.
3	Mercer Co.
6	Lawrence Co.
9	Butler Co.
5	Clarion Co.
1	Jefferson Co.
24	Beaver Co.
13	Allegheny Co.
9	Armstrong Co.
22	Indiana Co.
41	Washington Co.
19	Westmoreland Co.
1	Cambria Co.
6	Greene Co.
3	Fayette Co.
1	Somerset Co.

Fig. 1.—Middle Woodland Raccoon Notched point sites in New York and Pennsylvania.

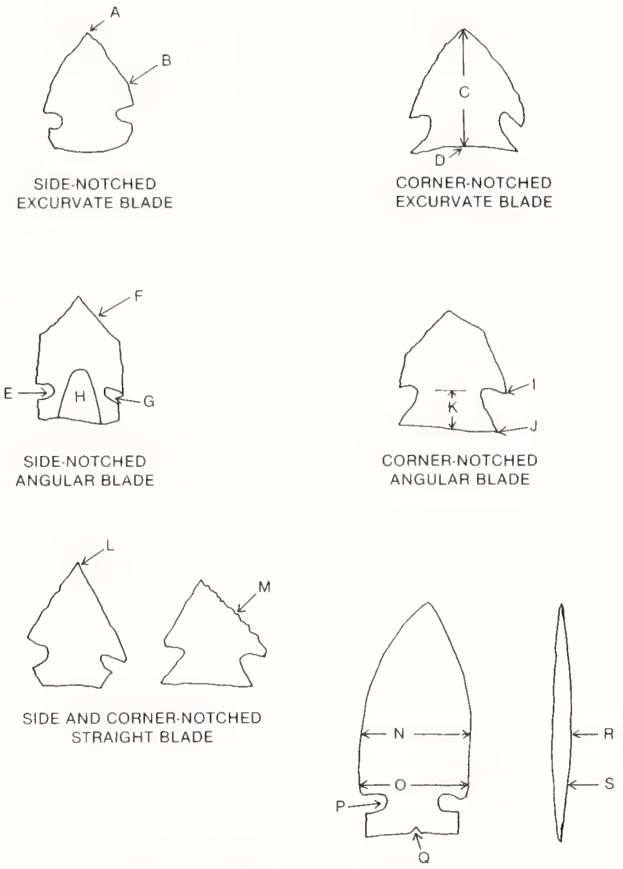


Fig. 2.—Standard projectile point terminology used in the text. A. Tip; B. Edge; C. Length; D. Base; E. Notch; F. Blade angle; G. Notch angle; H. Flute; I. Barb; J. Tang; K. Stem; L. Distal end; M. Serration; N. Blade width; O. Shoulder width; P. Notch depth; Q. Basal notch; R. Blade thickness; S. Stem thickness.

age in Erie County, Pennsylvania, as well. Subsequent survey work has now documented Raccoon Notched material along the upper Allegheny River in Warren County, Pennsylvania, as well as in New York's Chautauqua and Cattaraugus counties. While this indicates that the Raccoon Notched points are distributed throughout the Upper Ohio Valley, the tools are found in abundance at specific locations (Fig. 1). Concentrations of Raccoon Notched points were notable at the Beaver County Outdoor Theater site, 36 BV 24; three locations at Buckaloons in Warren County, 36 WA 29, 98 and 99; and at the Erie County Melnick site, 36 ER 31. The Middle Woodland lithics from these major sites provided a significant portion of the data base utilized to formulate the Raccoon point and tool typologies. This report, based on an interregional study initiated in 1980, fully defines and details the Raccoon Notched Point Assemblage and documents this important Middle Woodland manifestation in the Upper Ohio Valley.

METHODOLOGY

The Raccoon Notched Point Assemblage was defined through a laboratory study of provenienced specimens that were complete enough to be weighed and measured. The collections included in the analysis were either loaned or donated to the CMNH Division of Anthropology by the following field associates and regional representatives: Emil Alam, Beaver; Fran and William Ringlesbach, McDonald; William Stuart, Sugar Grove; and John Zavinsky, Warren, all from Pennsylvania, and William Buker, now of Tampa, Florida. Additional materials and information were obtained from Arnold Bailey, Meadville; William Bennington, Marianna; and M. Jude Kirkpatrick, Erie. The studied specimens represent over 250 accumulative years of collecting within the Upper Ohio Valley in Pennsylvania and a small quantity of Raccoon Notched artifacts retrieved by Buker from a comparable site in Muskingham County, Ohio (C-33 MU 34).

Over 5,500 sites recorded in the files of the Division of Anthropology at CMNH were reviewed for evidence of Middle Woodland occupation. These sites were identified by drawings, photographs, and listings of artifacts characterizing the period, namely, Snyders, Chesser, Steuben, Manker, Jack's Reef, and Raccoon Notched points. Documentation of chalcedony flake knives and ceramics was also culled from the files. Sites listed as being multicomponent were not included unless a direct informant interview confirmed a Middle Woodland occupation at any given locus. Rockshelters were eliminated entirely because of extreme variation in the information in the site files. For example, Warren County rockshelters were identified by time period but Venago County shelters were defined merely by name and location. Special consideration was also given to recently typed Middle Woodland points, including George's (1982) Garvers Ferry, Kiski Notched, and Murphys Stemmed and the Bennington Corner Notched (Quail Tail) point defined by Herbstritt (personal communication, 1986), and Boldurian (1985:171–172). All these latter types are too recent to appear in the CMNH site files. In these cases, all illustrations of points on site records were studied and the distributions of the newly defined point types were plotted. William Bennington confirmed site locations for the type that bears his name.

Known burial mounds within the Upper Ohio Valley in New York and Pennsylvania were also plotted. While these cannot be assigned to any given Woodland time frame, the mound structures fall into the same geographic settings as the open sites that were utilized by Middle Woodland cultures.

In all, 502 sites were identified as having Middle Woodland affiliations. Particular attention was paid to those sites that produced triangular points in association with components of the Raccoon Notched Point Assemblage and 160 sites were positively identified as having this association. The total count for sites with elements of the Raccoon Notched Assemblage is 236 and 68% of these sites have Raccoon Notched points in association with triangular points.

Collectors throughout the study area were interviewed and their collections were photographed and measured. Appendix I lists the provenience and collector for all artifacts included in the analysis, along with measurements, weights, lithic identification, and lithic sources. Research directed toward the project includes eight years of fieldwork in the French Creek drainage and along

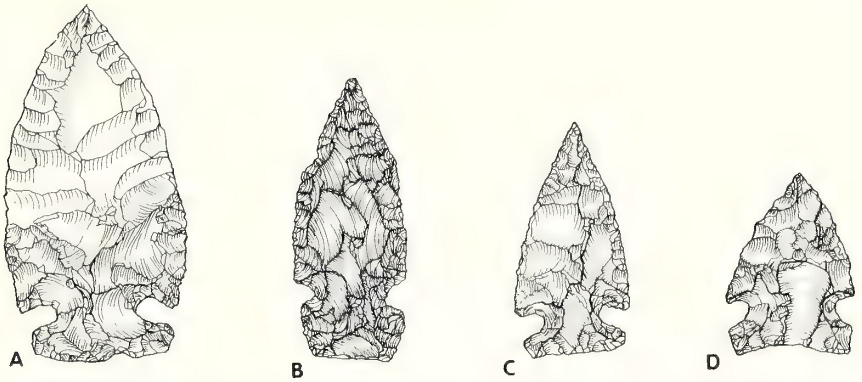


Fig. 3.—Type 1: Raccoon Side Notched points with excurvate blades. A. Onondaga, 36 WA 99; B. Coshocton, 36 VE 124; C. Flint Ridge, C-33 MU 34; D. Onondaga, 36 BV 24.

the Lake Erie Plain and 28 years of intensive site recording throughout western Pennsylvania and western New York.

To summarize, Middle Woodland archaeological sites are now identified by geographic location within counties and drainages of the Upper Ohio Valley. This confirms a considerable presence of Middle Woodland sites and burial mounds along major drainages in the western regions of Pennsylvania.

Since Mayer-Oakes (1955:97) recognized that Raccoon Notched projectile points occur with both side- and corner-notching, this basic structural difference was used to establish the initial categories in the assemblage. These two types were then separated according to variations in their configurations. Ultimately five types of projectile points were defined. These types are fully described and illustrated below along with four knife forms, four drill types, strike-a-lights, and scrapers, all considered to be part of the Raccoon Notched Point Assemblage. The terminology utilized in the descriptions of the types is shown in Fig. 2.

THE TYPOLOGY

Points

TYPE 1. Raccoon Side Notched Points with Excurvate Blades (Figs. 3, 4).

General description.—These are small, thin, side-notched points with an excurvate blade shape.

Measurements.—Thirty-six points representative of the variation within the type provided the measurements. Since 20 specimens from this group, mostly the larger points, have tip fractures, their lengths had to be estimated. Length of Type 1 ranges from 2.4 to 5.0 cm, averaging 3.6 cm; the majority (63%) are between 3.0 to 4.0 cm. The 16 unfractured points, or 44% of the total, range in length from 2.4 to 4.2 cm and average 3.2 cm. Width ranges from 1.6 to 2.8 cm and the majority (66%) fall between 2.0 to 2.5 cm. Thickness ranges from 3.0 to 6.0 mm, averaging 4.2 mm. Raccoon Notched points are distinctively thin. The majority (72%) of Type 1 range between 3.0 to 4.0 mm in thickness. Stem length ranges from 7.0 to 12.0 mm and averages 8.6 mm. Basal thickness ranges from 2.0 to 4.0 mm, averaging 2.7 mm.

Form.—In cross-section these side-notched points are often flattened but occasionally are plano-convex; the blade is excurvate with the edges occasionally finely serrated. The distal end is most often acuminate but is occasionally acute. The hafting area is side-notched with the notches ranging from 3.0 to 6.0 mm in depth and averaging 4.1 mm. The basal edge may be incurvate, straight, or excurvate; is usually thinned; and in most specimens is lightly ground. See Appendix I for other measurements.

Flaking.—The point preforms were either derived through the reduction of glacial pebbles by percussion flaking or fashioned from straight flakes struck from quarry blocks. The preforms were further shaped by the removal of broad, shallow, random flakes and retouched with fine finishing flakes. The base was thinned by the removal of one or more broad flakes, occasionally resulting in shallow fluting halfway up the length of the point. On some specimens, a narrow basal notch from the thinning process is visible. The basal edge evidences fine retouching. The notches were formed by the removal of broad flakes from the dorsal and ventral surfaces, generally resulting in deep, U-shaped notches. These notches were placed on the side of the hafting area from 0°, angling to 20° toward the basal edge.

Remarks.—The side-notched excurvate blade variety of the Raccoon Notched Type 1 point is the most numerous type in the total sample. These points are small in size, averaging only 3.6 cm in length with an average weight of only 2.9 g. This suggests that most of them were utilized on an arrow shaft.

A range of variation is recognized within this type. Although the blade edges are excurvate, the individual points vary, with the maximum width occurring across the base, on the shoulder, or as much as halfway up the blade. Thus the blade varies from egg-shaped to roughly triangular. A small percentage

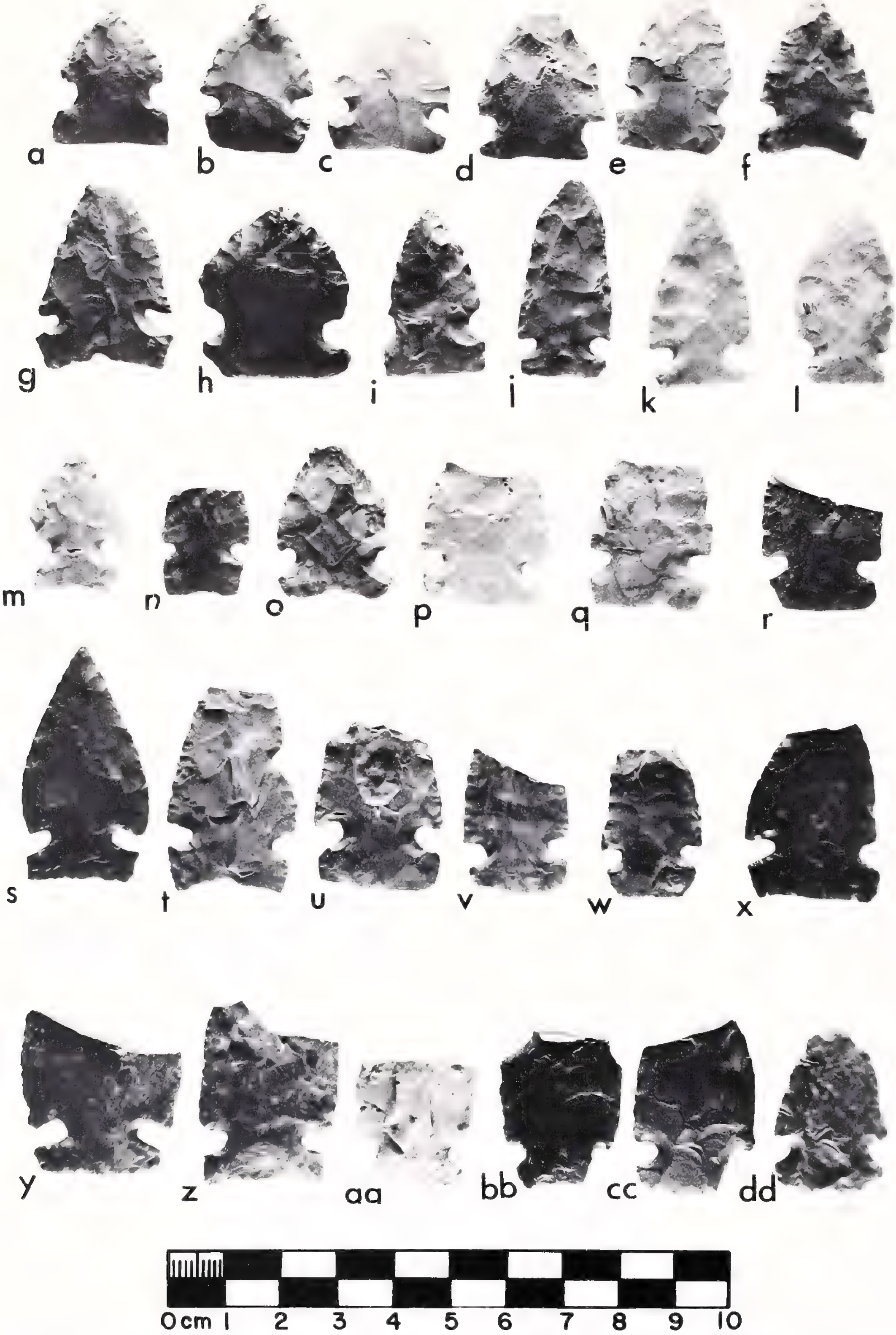


Fig. 4.—Type 1: Range of variation in Raccoon Side Notched points. a. Onondaga, 36 WA 98; b. Onondaga, 36 BV 24; c. Flint Ridge, 36 BV 24; d. Coshocton, 36 BV 24; e. Onondaga, 36 WA 99; f. Onondaga, 36 BV 24; g. Onondaga, 36 BV 20; h. Coshocton, 36 BV

of the type is asymmetrical and may have functioned as hafted knives.

Distribution.—Type 1 with side-notching is prevalent on all Upper Ohio Valley sites analyzed, ranging from 50% of all the related types at the Buckaloons sites to 70% at the Outdoor Theater site.

Variation within the type.—Type 1 is the major form of the Raccoon Notched point as described by Mayer-Oakes (1955:Plates 34, 35, 98). Its main characteristics are the somewhat equal length-to-width ratio, causing a stubby appearance, and its square to concave side-notched base.

Figures 3A and 4y show examples of a variant within Type 1, characterized by their ovate form and extreme central width. This same variant occurs in Type 2 with the only difference being the corner-notching. The variant seems to be widespread in western Pennsylvania, recorded at 36 BV 6, 36 BV 24, 36 ER 31, 36 WA 29, and 36 WA 99.

A second variation within Type 1 is illustrated in Figs. 3B and 4n. Similar to Ritchie's Long Bay point from the Canoe Point phase of early Point Peninsula in New York, dated at A.D. 240 ± 80 years, (Ritchie, 1971:125), this variant is a narrow, excurvate Raccoon Notched point that generally has an extended base. This is not a common form in the Upper Ohio Valley and is known mostly from the Buckaloons sites. The example in Fig. 3B is from the Polk Farm site, 36 VE 124, in Venango County.

Type 2. Raccoon Corner Notched Points with Excurvate Blades (Figs. 5, 6).

General description.—These are small, thin, corner-notched points with excurvate blades.

Measurements.—Twenty-five points representative of the variation within the type provided the following measurements: length ranges from 2.4 to 4.8 cm, averaging 3.7 cm, with the majority (68%) measuring between 3.0 and 4.3 cm. The width ranges from 2.0 to 2.9 cm, averaging 2.4 cm, and the majority (64%) are between 2.2 to 2.6 cm. Thickness ranges from 4.0 to 6.0 mm and averages 4.3 mm. Stem length is 7.0 to 10 mm and averages 9.0 mm. Basal thickness ranges from 2.0 to 3.0 mm, averaging 2.2 mm. The 14 unfractured points (56% of the sample) range from 2.4 to 4.6 cm in length to average 3.3 cm.

Form.—Often flattened and occasionally plano-convex in cross-section, this point has a blade that is excurvate with the edges occasionally plano-convex and sometimes finely serrated. The distal end is most often acuminate but is occasionally acute. The hafting area is corner-notched with the notches ranging from 3.0 to 7.0 mm in depth, averaging 5.2 mm. The basal edge may be incurvate, straight, or excurvate; is usually thinned and in most specimens is lightly ground. See Appendix I for other measurements.

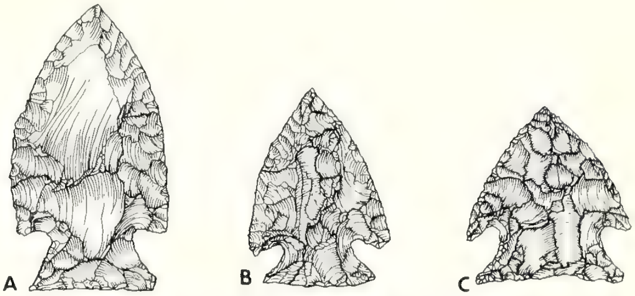


Fig. 5.—Type 2: Raccoon Corner Notched points with excurvate blades. A. Flint Ridge, 36 BV 20; B. Delaware, 46 HK 6; C. Coshocton, 36 AL 61.

Flaking.—The point preforms were derived through the reduction of glacial pebbles by percussion flaking, or else they were fashioned from straight flakes struck from quarry blocks. The preforms were further shaped by the removal of broad, shallow, random flakes and then retouched with fine, finishing flakes. The base was thinned by the removal of one or more broad flakes which occasionally resulted in shallow fluting extending up to half the length of the point. A small, narrow, basal notch from this fluting process is still present on some specimens. After thinning, the basal edge was finely retouched. The notches were formed by the removal of broad flakes from the dorsal and ventral surfaces, resulting in deep, expanding U-shaped notches. These notches were placed at or near the corner of the hafting area and this ultimately reduced the width of the basal edge.

Remarks.—The corner-notched excurvate blade variety of the Raccoon Notched point is the second most numerous type in the study. These points are essentially the same as Type 1; however, they are corner- rather than side-notched. A small percent-

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24; i. Onondaga, 36 BV 4; j. Onondaga, 36 WA 99; k. Flint Ridge, C-33 MU 34; l. Delaware, 36 WA 99; m. Delaware, 36 BV 24; n. Onondaga, 36 WA 99; o. Onondaga, 36 WA 99; p. Flint Ridge, 33 LI; q. Onondaga, 36 WA 99; r. Coshocton, 36 WA 99; s. Onondaga, 36 BV 6; t. Onondaga, 36 WA 29; u. Onondaga, 36 WA 98; v. Onondaga, 36 WA 99; w. Onondaga, 36 WA 99; x. Coshocton, 36 BV 9; y. Onondaga, 36 WA 99; z. Coshocton, 36 BV 24; aa. Delaware, 36 WA 31; bb. Coshocton, C-33 MU 34; cc. Coshocton, 36 WA 29; dd. Onondaga, 36 WA 99.

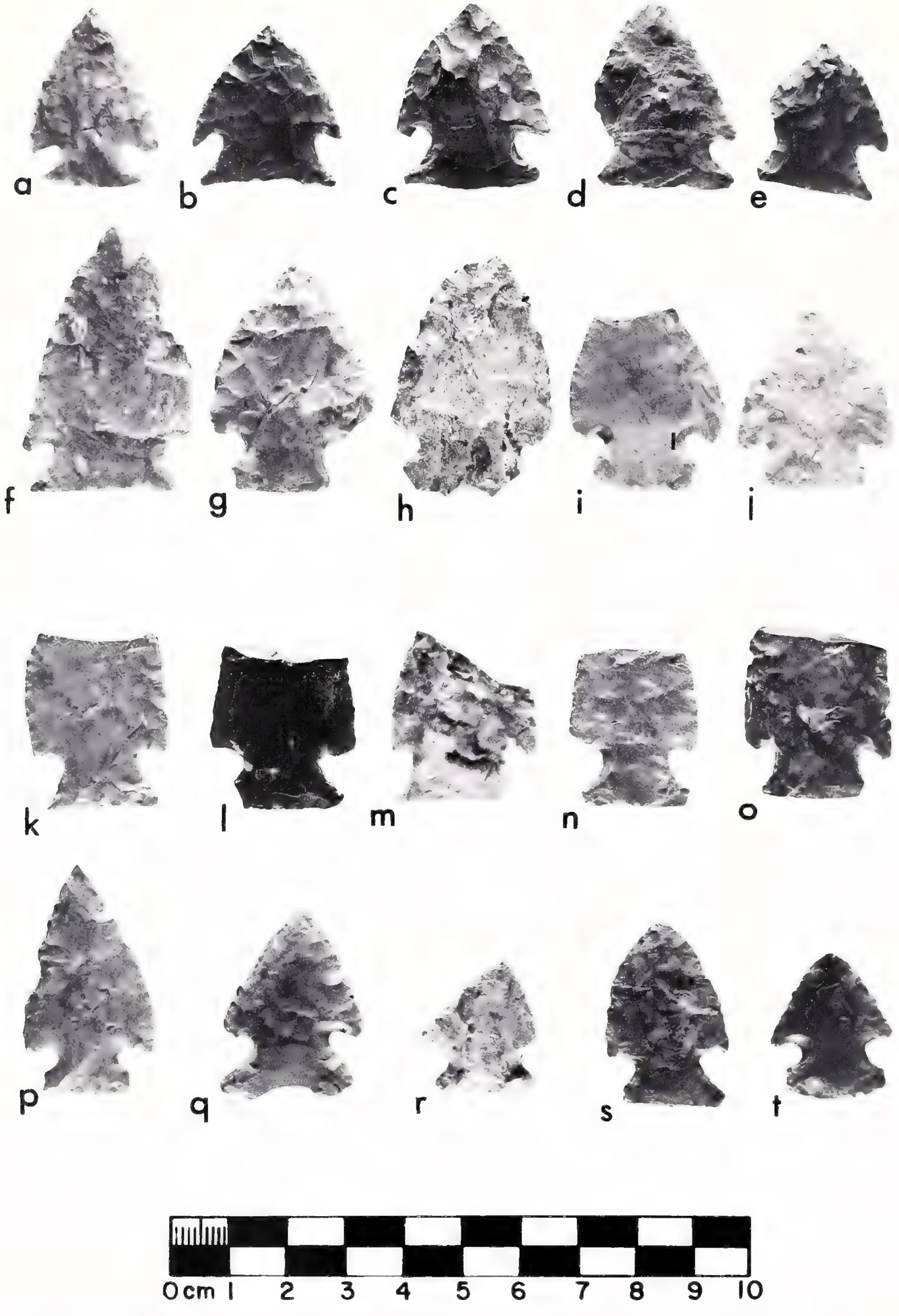

Fig. 6.—Type 2: Range of variation, Raccoon Corner Notched points. a. Coshocton, 46 HK 6; b. Coshocton, 36 AL 61; c. Coshocton, C-33 MU 34; d. Coshocton, C-33 MU 34; e. Coshocton, C-33 MU 34; f. Coshocton, C-33 MU 34; g. Onondaga, 36 WA 94; h. Coshocton, 36 BV 24; i. Onondaga, 36 WA 95; j. Coshocton, 36 BV 23; k. Coshocton, 36 BV 20; l. Coshocton, 36 BV 25; m. Coshocton, 36 BV 111; n. Coshocton, 36 BV 25; o. Coshocton, C-33 MU 34; p. Onondaga, 36 WA 98; q. Onondaga, 36 WA 98; r. Onondaga, 36 WA 99; s. Onondaga, 36 WA 99; t. Onondaga, 36 WA 98.

age of the type appear to have served as knives. As is the case with Type 1, a high percentage of the larger-sized forms are fractured and lengths had to be estimated. The average length of 3.3 cm and the light weight, averaging only 3.8 g, suggest that this point type was related to the use of the bow and arrow.

Distribution.—Type 2 is distributed throughout the Upper Ohio Valley but is more prevalent in the north. The Outdoor Theater site in Beaver County produced only 3% of the type, while the Buckaloons sites in Warren County have 21 to 29% and the Melnick site in Erie County yielded 25% of the Type 2 forms. The significance of this percentage difference cannot be addressed at the present time; however, it may reflect a variation that is either regional or timed to a specific portion of the Middle Woodland period.

Type 2 of the assemblage is comparable to the Alabama Corner Notched Woodland type, one of which was obtained at Russell Cave in Jackson County, Alabama, and dated around A.D. 450 (Cambron and Hulse 1969:69).

Variation within the type.—There are three variants of Type 2; the first is shown in Figs. 5A and 6k–o. It is characterized by its long, slender appearance, occasionally having almost straight parallel sides with corner-removed notching. This variant is more common in Beaver County, Pennsylvania, and is rare in the northern counties of the state. It is also present in the Buker collection from site C-33 MU 34, Muskingham County, Ohio. The variant is comparable to the larger version of the Jack's Reef Corner Notched point (Ritchie, 1965: Plate 80, No. 20). It is not known why the distribution of the variant is exactly opposite to that of Type 2 as a whole.

The second variant, shown in Figs. 5B and 6a and f, is generally smaller and exhibits narrower corner-notching than most of the Type 2 points. The third variation within Type 2 is shown in Figs. 5C and 6b–e. It is most numerous at the Melnick site in Erie County (Fig. 25g–i). Most similar to the side-notched Type 1D, it is characterized by an almost equal length-to-width ratio and a large corner-removed notch. The last two variants are minor to rare on Raccoon Notched point sites and are similar to the Jack's Reef Corner Notched point (Ritchie, 1971: Plate 11, No. 13).

Type 3. Raccoon Pentagonal Side Notched Points (Figs. 7; 8a–g, i–n).

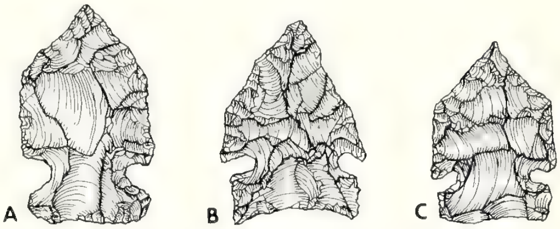

Fig. 7.—Type 3: Raccoon Pentagonal Side Notched points. A. Delaware, 36 WA 98; B. Coshocton, 36 BV 24; C. Coshocton, C-33 MU 34.

General description.—These are small, thin, side-notched points having angular edges.

Measurements.—Fifteen points representative of the variation within the type provided following measurements: length ranges from 2.2 to 3.8 cm, averaging 2.9 cm. The majority (80%) measure between 2.5 to 3.5 cm. The width ranges from 1.8 to 2.6 cm, averaging 2.1 cm. The majority (66%) measure between 2.0 to 2.3 cm. Thickness ranges from 3.0 to 5.0 mm, averaging 4.0 mm, and stem length ranges from 7.0 to 11.0 mm with an average of 8.4 mm. Basal thickness ranges from 2.0 to 3.0 mm, averaging 2.5 mm.

Form.—In cross-section this type is often flattened but is occasionally plano-convex. The blade is angular and pentagonal with the edges occasionally finely serrated. The distal end is most often acuminate but occasionally it is acute. The hafting area is side-notched with the notches ranging in depth from 3.0 to 5.0 mm, averaging 4.0 mm. The basal edge may be incurvate, straight, or excurvate; is usually thinned; and in most specimens is lightly ground. See Appendix I for other measurements.

Flaking.—Basically, this point type was manufactured in the same manner as was Type 1; however, it was retooled toward the distal end by the removal of flakes for an unknown specialized function. A straight edge was maintained in the flaking process, giving the point an angular look and reducing the length of the blade.

Remarks.—This point type is less common than Types 1 and 2. Within the type, variation is recognized, with some specimens exhibiting equilateral, angular edges and others having blade edges of unequal length and angle. The average length of this type (2.9 cm) is less than the 3.6 cm of Type 1 and the 3.8 cm of Type 2. This shortness may have resulted from resharpening a tip-fractured point to convert it into some kind of specialized tool—possibly even a retooled cutting instrument on its original shaft.

Distribution.—Type 3 is found throughout the Upper Ohio Valley but it occurs in its highest fre-

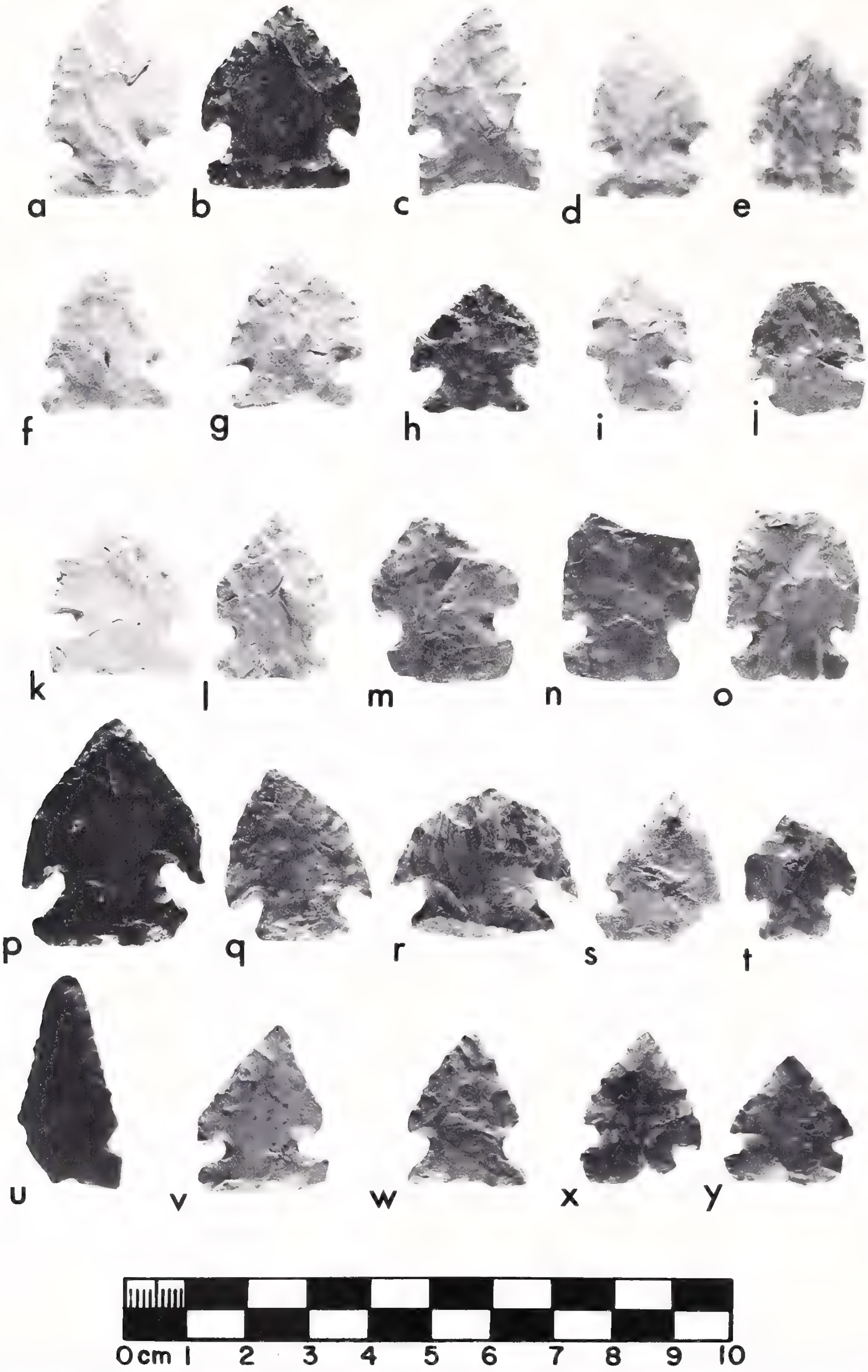

Fig. 8.—Range of variation in Raccoon Pentagonal Side Notched points. Type 3: Raccoon Pentagonal Side Notched points: a. Delaware, 36 WA 98; b. Coshocton, 46 HK 6; c. Coshocton, 36 BV 24; d. Coshocton, C-33 MU 34; e. Coshocton, C-33 MU 34; f. Onondaga, 36 BV 24; g. Onondaga, 36 WA 96; i. Onondaga, 36 WA 99; j. Onondaga, 36 WA 99; k. Flint Ridge, C-33 MU 34; l. Coshocton, 36 BV 24; m. Onondaga, 36 WA 31; n. Onondaga, 36 WA 31; o. Onondaga, 36 WA 29. Type 4: Raccoon Pentagonal Corner Notched points: h. Coshocton, 36 BV 24; p. Coshocton, 33 LI; q. Onondaga, 36 BV 24; r. Coshocton, 46 HK 34; t. Onondaga, 36 WA 95. Type 5: Raccoon Notched Side and Corner Notched points on straight blades: s. Coshocton, 36 BV 24; u. Unknown, 36 BV 24; v. Onondaga, 36 WA 99; w. Onondaga, 36 WA 99; x. Coshocton, 36 BV 24; y. Onondaga, 36 WA 90.

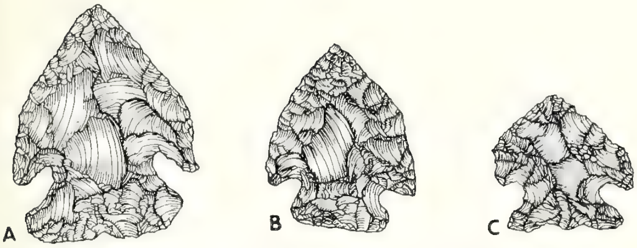

Fig. 9.—Type 4: Raccoon Pentagonal Corner Notched points. A. Coshocton, 33 LI; B. Onondaga, 33 BV 24; C. Coshocton, 36 BV 24.

quency at the Outdoor Theater site in Beaver County, Pennsylvania. This pentagonal form has been included within the Jack's Reef typology (Ritchie, 1971:26, and Plate 11).

Variation within the type.—Many of the Type 3 points appear to have been subjected to extensive retooling, resulting in a wide range of variation within the type. On Fig. 7, A and C are symmetrical whereas B has a short angular blade on the left and a long, straight blade on the right.

Type 4. Raccoon Pentagonal Corner Notched Points (Figs. 8h, p–r, t; 9).

General description.—These are small, thin, corner-notched points having angular edges.

Measurements.—Eight points representative of the variation within the type provided the following measurements: length ranges from about 2.0 to 3.8 cm, averaging 2.9 cm. The width ranges from 1.8 to 3.0 cm, averaging 2.3 cm, and thickness ranges from 4.0 to 5.5 mm with the average being 4.6 mm. Stem length ranges from 7.0 to 9.0 mm, averaging 7.6 mm, and the basal thickness ranges from 2.0 to 3.0 mm, averaging 2.3 mm.

Form.—In cross-section this type is often flattened but occasionally is plano-convex. The blade is angular, pentagonal, and occasionally finely serrated. The distal end is most often acuminate but sometimes it is acute. The hafting area is corner-notched with the notches ranging in depth from 4.0 to 7.0 mm, averaging 5.5 mm. The basal edge may be incurvate, straight, or excurvate; is usually thinned; and in most specimens is lightly ground. See Appendix I for other measurements.

Flaking.—This point type was manufactured in a similar manner as was Type 2; however, it was retooled toward the distal end by the removal of flakes for an unknown specialized function. A straight edge was maintained in the flaking process, giving the point an angular look and reducing the length of the blade.

Remarks.—This minority type varies from Type 3 by being corner- rather than side-notched.

Distribution.—Type 4 points were recovered at the Outdoor Theater site in Beaver County (13% of the total recovered), at Buckaloons in Warren County (36 WA 29, 13%; 36 WA 99, 6%), and at the Melnick site in Erie County (4%).

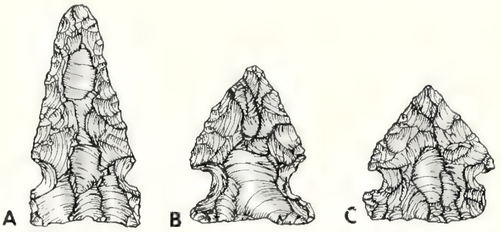

Fig. 10.—Type 5: Raccoon Side and Corner Notched points on straight blades. A. Unknown, 36 BV 24; B. Onondaga, 36 WA 29; C. Onondaga, 36 WA 90.

Type 5. Raccoon Side and Corner Notched Points on Straight Blades (Figs. 8s, u–y; 10).

General description.—These are small, thin, side- and corner-notched points having straight edges.

Measurements.—Eight points representative of the variation within the type provided the following measurements: length ranges from 1.7 to 3.5 cm, averaging 2.6 cm. The majority (63%) are between 2.0 to 3.0 cm. The width ranges from 1.7 to 2.3 cm, averaging 2.0 cm, with the majority falling between 1.8 and 2.0 cm. Thickness ranges from 3.0 to 5.0 mm, averaging 4.1 mm. Stem length ranges from 6.0 to 8.0 mm, averaging 7.2 mm. Basal thickness ranges from 2.0 to 3.0 mm with the average being 2.3 mm.

Form.—In cross-section this type is often flattened but occasionally is plano-convex. The blade is straight—or almost so—with the edges occasionally serrated. The distal end is most often acuminate but sometimes it is acute. The hafting area is side- or corner-notched with the notches ranging in depth from 2.0 to 5.0 mm, averaging 3.8 mm. The basal edge may be incurvate, straight, or slightly excurvate; is usually thinned; and in most specimens is lightly ground. See Appendix I for other measurements.

Flaking.—Essentially, this point type was produced in the same manner as Types 1 and 2; however, the distal end was tooled to a straight edge from the tip to the notch by the removal of additional flakes, occasionally spaced so as to leave the edge serrated.

Remarks.—Because of the small sample, both corner- and side-notched varieties were included within this type. The blades may have been reworked until the angular edges intersected the notches. This type may have had its origin in Types 3 and 4. Occasionally these points, as well as some of the other types, exhibit a small thin notch somewhere along the basal edge. See the illustrations of Types 2, 3, and 4.

Raccoon Notched Points as Arrow Points

For years archaeologists have speculated about the beginning date for the use of the bow and arrow. Many have concluded that the bow and arrow emerged during the Middle Woodland period but this is difficult to prove, especially in the Northeast where perishables are rarely preserved and sufficient radiocarbon dates are lacking. Generally all that remains for study is a complex assortment of stone projectile points, and it is difficult to determine if these tools are associated with javelins, atlatls and darts, or bows and arrows.

The weight and size of a given stone projectile point do not positively determine function. Many Archaic points such as the LeCroy are often as small and as thin as points utilized in later Woodland times. Therefore, many of the assumptions made when attempting to date the origin of the bow and arrow in North America have been derived from historic evidence and rely on comparisons of prehistoric lithics with modern arrowheads. Sporting goods stores report that the weight of the modern steel arrowhead ranges from 8 to 10 g. The five types of Raccoon Notched points average 3.1 g, or one-third the weight of the modern steel arrowhead. Chipped stone projectile points that can be mounted on a split or notched shaft are generally not more than 5 mm in thickness, well above the average thickness (2.3 mm) of the Raccoon Notched points. Heavier and larger stone points, when used on arrow shafts, are thought to have been mounted with a socket arrangement (Hamilton, 1982:27).

Some of the heaviest arrow shafts and point tips known were used by nineteenth- and twentieth-century Columbian Indians in South American rain forests. Their short-range arrows were mounted with thin iron arrowheads weighing up to 15 g, or over twice as much as the heaviest Raccoon Notched point at 6.8 g (Hamilton, 1982:54–65).

Perhaps more relative to establishing the beginning date for the bow and arrow and the use of Raccoon Notched points as arrow tips is the known association of the Raccoon Notched points with the triangular Levanna points. The association of Levanna points with Jack's Reef Corner Notched varieties is well documented by Ritchie in New York, where the Levanna point emerged around A.D. 700. Ritchie noted that the Raccoon Notched points bear resemblances to the Jack's Reef forms and he further projected his belief that Levanna and Jack's Reef points were utilized as arrow points (Ritchie, 1965: 243; 1971:32).

Furthermore, Bell (1958:76, 77) listed the side-notched Reed point of the Gibson and Fulton aspect in Oklahoma (A.D. 500 to A.D. 1500) as an arrow point. The similarity of this point to the Raccoon Notched Type 1C (Fig. 3) has already been noted.

The concept that at least some of the Raccoon Notched and associated Levanna points were used on arrow shafts is supported by data in this report. The thinness of the points suggests they were fashioned for mounting on small shafts. Furthermore, the weight and small size support the postulated function as arrowheads. It is reasonable to assume that the somewhat abrupt appearance of triangular points in Pennsylvania around A.D. 600 was the time that the bow and arrow was introduced.

Knives

Knives were divided into four types by their configuration and attributes. The validity of the classification as knives rather than preforms or points requires some definition. The concept that blades utilized as knives would be asymmetrical was applied in the analysis and the tools were examined for evidence of fine retouching, edge wear, and edge beveling. The Type 1 knives, for example, have one straight edge, sometimes angular to curved. The opposite blade edge curves more sharply to the tip and the blades are asymmetrical in form. On all Type 1 specimens, the cutting edge is finely flaked with the high points showing edge wear under microscopic examination. Preforms would not have these attributes; nor would finished points be intentionally asymmetrical. All illustrated examples were verified as having been utilized as knives through examination under a binocular microscope.

TYPE 1. Raccoon Excurvate Knives (Figs. 11; 12a, b, d, e, k–m).

General description.—These are thin, unnotched knife blades with an excurvate shape. When one looks at their length and width, they are proportionately wider than other tools.

Measurements.—Few complete specimens were available for measurement; of the 65 blades examined in the total study, 15 were complete enough to be placed in this category. As far as can be determined, the measurements of these blades closely conform with those of the Raccoon Notched point Types 1 and 2. Blade length ranges from 2.4 to 5.0 cm; the width from 1.6 to 2.9 cm; and thickness from 3.0 to 6.0 mm.

Form.—In cross-section the excurvate knife is often flattened but occasionally is plano-convex. The blades have excurvate and generally asymmetrical edges that sometimes are finely serrated. The distal end is most often acuminate but occasionally it is acute. The hafting area is unnotched, with its length generally determined by the presence of edge grinding. The basal edge may be incurvate, straight, or excurvate; is usually thinned; and in most specimens is lightly ground.

Flaking.—The knife preforms were either derived through the reduction of glacial pebbles by percussion flaking or fashioned from straight flakes struck from quarry blocks. The preforms were further shaped by the removal of broad, shallow, random flakes followed by retouching. The base was thinned by the removal of one or more broad flakes, occasionally resulting in shallow fluting on up to half the length of the blade. The basal edge and hafting area were finely retouched.

Remarks.—This knife type in all its various forms differs little from the Type 1 point, other than the lack of notches. If symmetrical, these knives could easily pass as point preforms. Type 1B is similar in form to the Jack's Reef Pentagonal points described by Ritchie (1971:28). This knife form is generally broader than Type 2; however, it could morphologically grade into the lanceolate form described below. Knives similar in form are illustrated in Ritchie (1965:Plates 81, 88).

Type 2. Raccoon Lanceolate Knives (Figs. 12f–j; 13).

General description.—These are long, thin, unnotched knife blades that are lanceolate in form and have a greater length-to-width ratio. Specimens often have a straight edge opposite a more curved edge. All examples have fine retouching and edge wear.

Measurements.—Few complete specimens were available; however, of the 65 blades in the total study sample, 15 were complete enough to be assigned to this type. As far as can be determined, the blades range in length from 3.8 to 6.0 cm; in width from 2.0 to 2.5 cm; and in thickness from 3.0 to 5.0 mm.

Form.—In cross-section Type 2 knives are often flattened but occasionally are plano-convex. The blade edges tend to be parallel above the base; however, toward the distal end, one edge is often straight and the other excurvate. The hafting area is unnotched, with its length determined by the presence of light edge grinding. The distal end is most often acuminate and the basal edge is straight to slightly excurvate and seldom incurvate. The base has been thinned on all specimens.

Flaking.—Essentially, the preform of this knife was manufactured in the same manner as Type 1; however, it was fashioned from either a larger glacial flint pebble or a large quarry block flake to produce the longer blade. Very fine and controlled finishing flakes were removed from the basal edge and from the hafting area.

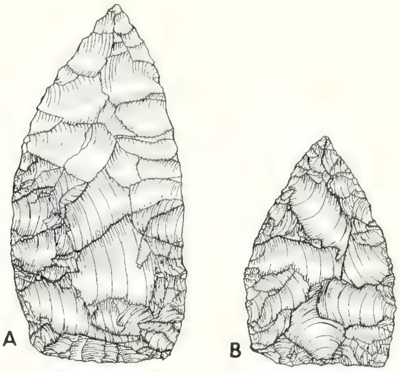

Fig. 11.—Type 1: Raccoon Excurvate knives. A. Onondaga, 36 WA 29; B. Coshocton, 33 LI.

Remarks.—This knife form is generally more than twice as long as it is wide; however, some specimens could grade morphologically into the Type 1 knife forms. Ritchie (1965:Plates 81, 88) illustrates several knives of this type.

Type 3. Raccoon Pentagonal Knives (Figs. 12c, n–o; 14).

General description.—These are thin, unnotched pentagonal knife blades with angular edges.

Measurements.—Few complete specimens were available for measurement; however, of the 65 blades examined in the total study, ten were complete enough to be placed in this category. As far as can be determined, the measurements of these blades would conform with those of the Raccoon Notched point Types 3 and 4. The length of the pentagonal knives range from 2.0 to 3.8 cm, width from 1.8 to 3.0 cm, and thickness from 3.0 to 5.0 mm.

Form.—In cross-section these knives are often flattened and occasionally are plano-convex. The blade edges are angular, pentagonal, and occasionally finely serrated. The distal end is acuminate but sometimes it is acute. The hafting area is unnotched and generally lightly ground. The basal edge may be incurvate or excurvate, but it is generally straight, usually thinned, and in most specimens lightly ground.

Flaking.—This knife type was manufactured in a similar manner to Type 1; however, it was retooled toward the distal end by the removal of finishing flakes for an unknown, specialized function. A straight edge was maintained during the flaking pro-

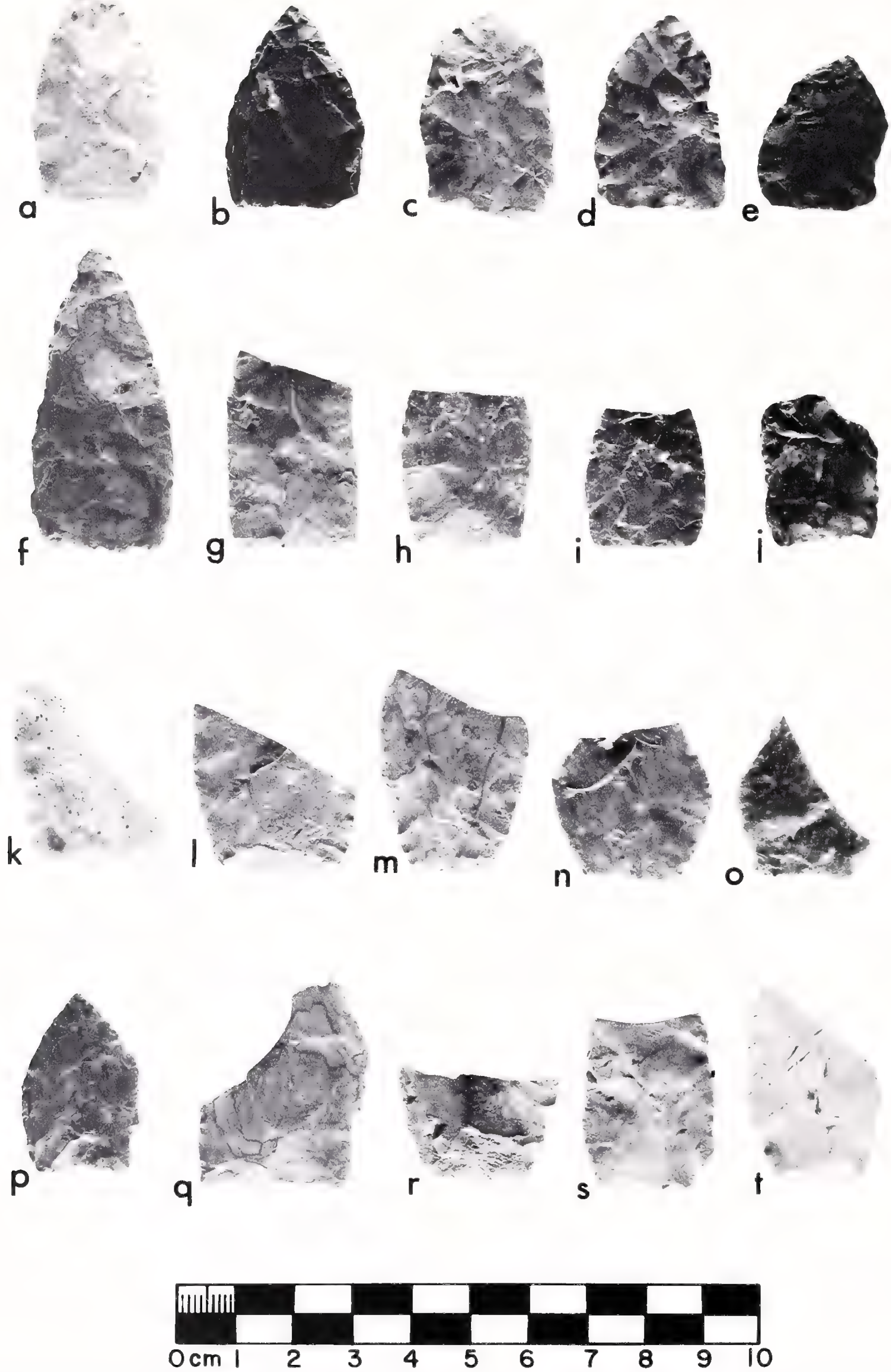

Fig. 12.—Range of variation of Raccoon Excurvate knives. Type 1: Raccoon Excurvate knives: a. Delaware, 36 WA 99; b. Coshocton, 33 LI; d. Onondaga, 36 WA 98; e. Unknown, 36 WA 98; k. Flint Ridge, 36 BV 24; l. Onondaga, 36 WA 99; m. Onondaga, 36 WA 98. Type 2: Raccoon Lanceolate knives: f. Onondaga, 36 WA 99; g. Onondaga, 36 WA 99; h. Onondaga, 36 WA 99; i. Coshocton, 36

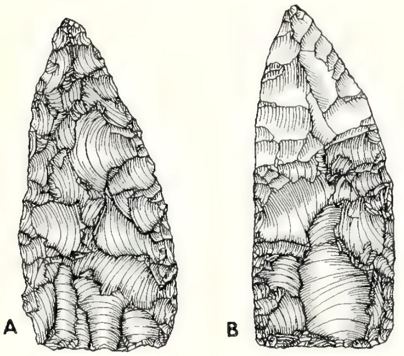

Fig. 13.—Type 2: Raccoon Lanceolate knives. A. Onondaga, 36 WA 99; B. Onondaga, 36 WA 99.

cess, giving the knife an angular look and reducing the length of the blade.

Remarks.—Other than the missing notches, this knife type is similar in form to point Types 3 and 4 and, when nearly symmetrical, would compare to the Jack's Reef Pentagonal point (Ritchie, 1971:80). Ritchie's illustrated examples are not symmetrical and appear to be knives rather than projectile points. Tools similar to the pentagonal knife form are included in the taxonomy of the Intrusive Mound Culture of Ohio (Morgan, 1952:93; Seeman, 1980: 11). This pentagonal knife is the most controversial of the four defined types. Ritchie (1971:28) has classified the pentagonal forms as Jack's Reef Pentagonal points. Others have suggested that these blades are preforms for pentagonal corner- and side-notched points. The typing as knives is based on asymmetry, edge wear, and beveling on finely retouched edges. Complete knives of this type are extremely rare; only three were complete enough for measurements and these were all from the Buckaloons sites in Warren County, Pennsylvania. If a larger sample was available for study, the suggestion that some specimens were projectile points could be validated.

Type 4. Raccoon Corner Removed Knives (Figs. 12p–t, 15).

General description.—These are thin, corner-removed knife blades with excurvate to angular edges.

Measurements.—Few complete specimens were available; however, ten corner-notched forms were recognized in the total sample of 65 knives. The blades range in length from 3.2 to 5.0 cm; in width from 2.0 to 3.0 cm, and in thickness from 3.0 to 5.0 mm.

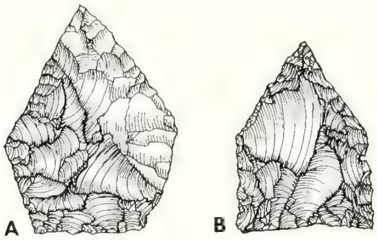

Fig. 14.—Type 3: Raccoon Pentagonal knives. A. Coshocton, 36 BV 9; B. Onondaga, 36 WA 99.

Form.—In cross-section the Type 4 knives are often flattened and occasionally are plano-convex. The blade edges may be excurvate to angular, are generally asymmetrical, and sometimes finely serrated. The distal end is most often acuminate but occasionally it is acute. The hafting area was created by the removal of one corner and blade edge, leaving a weak, horizontal to tapered shoulder and an incipient stem. The hafting area ranges in length from 5.0 to 13.0 mm. The basal edge is straight, excurvate, or incurvate, and is thinned on all specimens. The basal edge and hafting area are lightly ground.

Flaking.—Basically, the preform for this knife was produced in the same manner as Type 1; however, the hafting area received special treatment by the removal of fine finishing flakes along one side of the stem edge.

Remarks.—The removal of one corner and stem edge is the distinguishing factor in identifying the Type 4 knife; otherwise it resembles all of the preceding knife types. This type is represented in collections from the Buckaloons, Outdoor Theater, and Melnick sites.

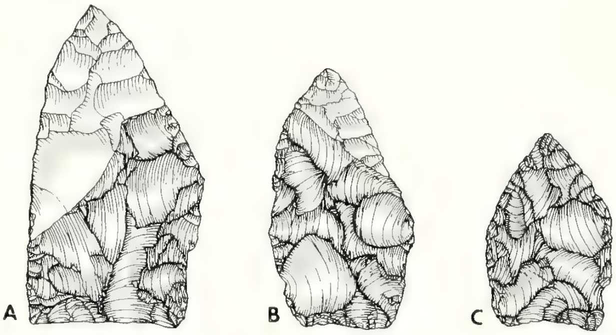

Fig. 15.—Type 4: Raccoon Corner Removed knives. A. Flint Ridge, 36 BV 24; B. Onondaga, 36 WA 99; C. Onondaga, 36 WA 99.

←

BV 9; j. Coshocton, 36 BV 24. Type 3: Raccoon Pentagonal knives: c. Onondaga, 36 WA 98; n. Onondaga, 36 BV 24; o. Coshocton, 36 BV 9. Type 4: Raccoon Corner Removed knives: p. Onondaga, 36 WA 99; q. Flint Ridge, 36 BV 24; r. Onondaga, 36 WA 98; s. Onondaga, 36 WA 98; t. Delaware, 36 WA 99.

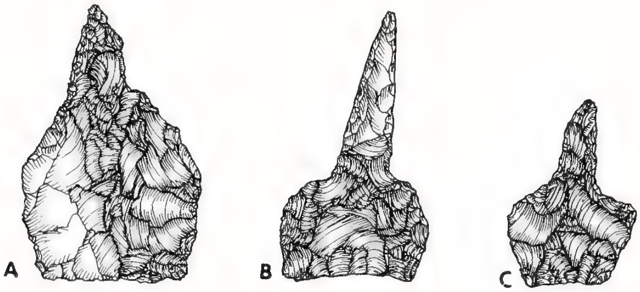

Fig. 16.—Type 1: Raccoon Ovoid Base drills. A. Delaware, 36 BV 24; B. Coshocton, 36 BV 9; C. Onondaga, 36 WA 91.

Drills

All of the drill types were manufactured from preforms, some of which resisted lateral thinning. The configurations of the bases divide the drills into four types:

Type 1. Raccoon Ovoid Base Drills (Figs. 16; 17a, b, d).

General description.—These are thin, ovate-base drills with slender bits.

Measurements.—Many specimens in various collections were examined by the author; however, only four complete drills of this type were available for measurement. The largest complete specimen was 4.6 cm in length. The basal length of one ovate-base drill was 3.2 cm, while the width was 3.9 cm.

Form.—In cross-section the base is thin and biconvex and the bit is narrow and diamond-shaped. The distal end is most often acuminate. The hafting area is always contracting and unnotched and most often is lightly ground. The basal edge is straight, occasionally incurvate, and thinned on all specimens.

Flaking.—The production of these thin drills is identical to that of the Type 1 knife.

Remarks.—The base of this drill simulates the form of the Type 1 knife.

Variation within the type.—There are three variants of the Type 1 drill. Specimens shown on Figs. 16A and 17b were manufactured from an ovate preform with the maximum thickness being at the juncture of the extended base and bit, suggesting the recycling of point or knife preforms that could not be thinned for proper use as their first intended function. The main characteristic is a long, wide base with a short bit. A second variant (Figs. 16B; 17a, d) has the same basal configuration; however, the bit has been extended, thus shortening the base. The third variant (Fig. 16C) is recognized by its narrow basal edge, suggesting manufacture from an ovate preform.

Type 2. Raccoon Rectangular Base Drills (Figs. 17c, 18).

General description.—These are thin, rectangular drills with T-shaped bases and slender bits.

Measurements.—Although many specimens are present in various collections, only one complete drill was available for measurement. This specimen measures 4.2 cm in length. All smaller specimens have broken bits; however, the length range probably coincides with the knife types. In width, the rectangular-base drills range from 1.8 to 2.7 cm and the length of the base ranges betwen 14.0 and 19.0 mm.

Form.—In cross-section the base is thin and biconvex; the bit is narrow and diamond-shaped. The unnotched hafting area is parallel to contracting but occasionally is expanding. Most specimens evidence light basal grinding. The basal edge is straight to incurvate, seldom excurvate, and thinned on all specimens studied.

Flaking.—The drill preforms were derived through the reduction of glacial pebbles by percussion flaking, or else they were fashioned from straight flakes struck from quarry blocks. The preforms were further shaped by the removal of broad, shallow, random flakes, and the blade sections were reduced by the removal of small, short, and thick flakes to leave a narrow bit section. The base was thinned by the removal of one or more broad flakes. Both the hafting area and the basal edges were retouched with fine finishing flakes.

Remarks.—Many of the bases of these drills resemble the bases found on Types 2 and 3 knives. This type shows variation in the length of the bits; however, the main characteristic is the parallel-sided base. The type also exhibits unusual thickness at the base of the bit.

Type 3. Raccoon Side and Corner Notched Base Drills (Fig. 19).

General description.—These are side- and corner-notched points with the blades retooled into drill bits.

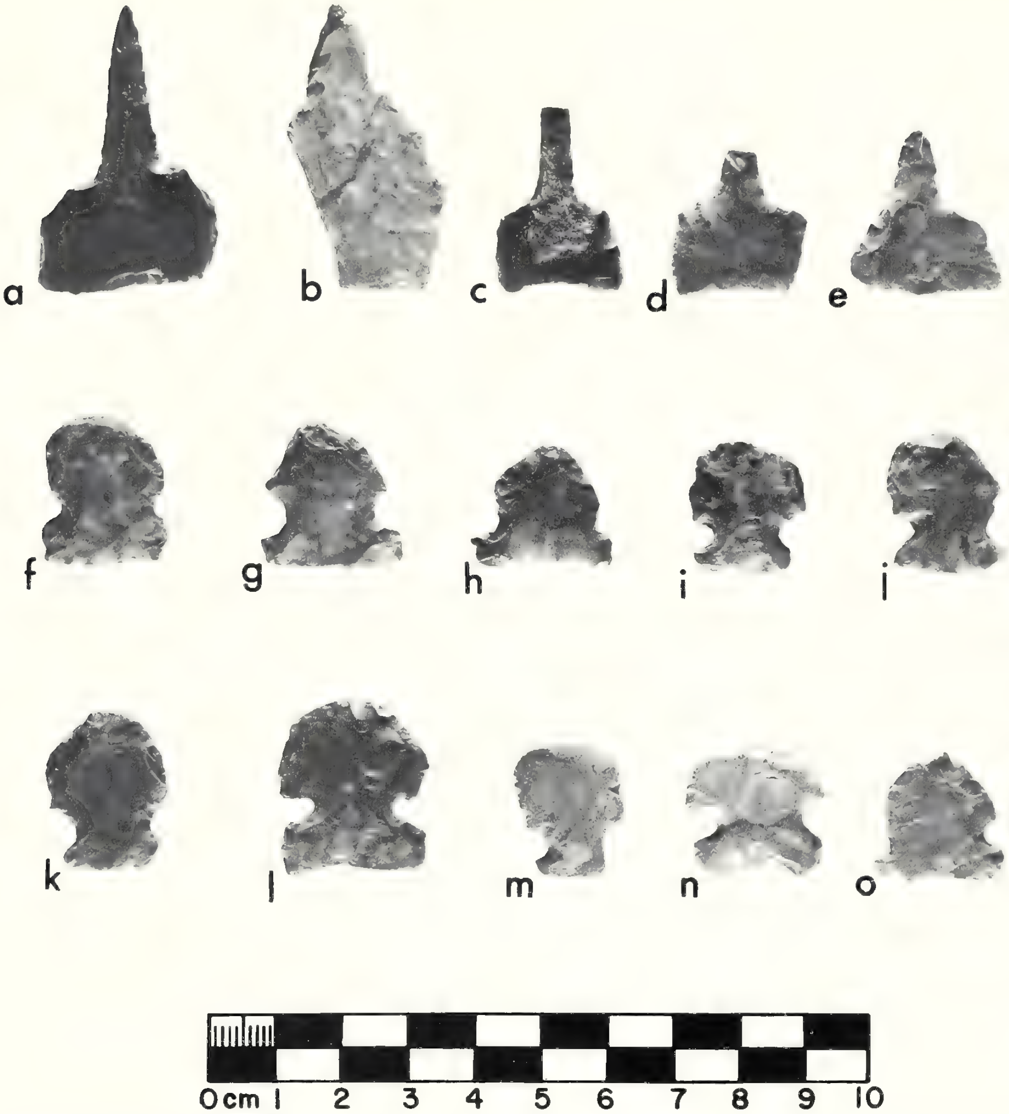

Fig. 17.—Range of variation, Raccoon Ovoid Base drills, strike-a-lights, and scrapers. Type 1: Raccoon Ovoid Base drills: a. Coshocton, 36 BV 9; b. Delaware, 36 BV 24; d. Coshocton, 36 BV 24. Type 2: Raccoon Rectangular Base drill: c. Coshocton, 36 BV 24. Type 4: Raccoon Triangular Base drill. e. Onondaga, 36 BV 24. Type 1: Raccoon Side and Corner Notched strike-a-lights: f. Onondaga, 36 WA 99; g. Onondaga, 36 WA 99; h. Onondaga, 36 BV 24; i. Onondaga, 36 WA 98; j. Onondaga, 36 WA 99. Type 1: Raccoon Side and Corner Notched scrapers: k. Onondaga, 36 WA 99; l. Onondaga, 36 BV 9; m. Onondaga, 36 BV 98; n. Onondaga, 36 BV 24; o. Delaware, 36 BV 24.

Measurements.—Eight complete specimens were available for measurement. With the exception of the retooled blade section, all measurements coincide with the point types. These drills are unusually thick at the point of expansion at the base of the bit, measuring from 0.6 to 1.0 cm, evidently being recycled from point rejects that were too thick for hafting.

Form.—With the exception of the bit, the side- and corner-notched drills simulate the point types.

Flaking.—The drills are flaked in the same manner as the point types; the upper blade has been reduced by the removal of small, short, and thick flakes to produce a narrow bit.

Remarks.—The bit of the side- and corner-notched base drills is often extremely acute and may have functioned as a reamer. These drills were often manufactured from point preforms of point Type 5c, and in some cases it is difficult to distinguish these from the Type 4 drills, made from triangular points, because of occasional shallow notching on the Type 3 drills.

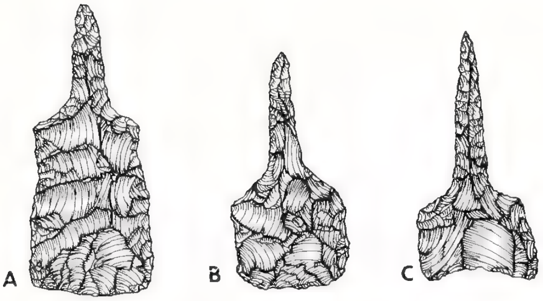

Fig. 18.—Type 2: Raccoon Rectangular Base drills: A. Onondaga, 36 WA 99; B. Onondaga, 36 WA 99; C. Coshocton, 36 BV 24.

Type 4. Raccoon Triangular Base Drills (Figs. 17e, 20).

General description.—These are drills with triangular bases.

Measurements.—Although many specimens are found in collections, only 11 were complete enough for measurement. The largest complete specimen is 4.0 cm in length while the smallest is 2.0 cm. In width, they range from 1.6 to 3.5 cm while thickness ranges from 0.4 to 1.0 cm with the majority measuring over 0.7 cm.

Form.—These drills were derived from triangular points or triangular point rejects; therefore, their size and shape varies.

Flaking.—The base sections were reduced by the removal of broad, shallow, random flakes. The blade sections were reduced by the removal of small, thick flakes to narrow the bit, but leaving the bit thicker than the base.

Remarks.—Triangular drills are distinguished from points by the presence of polish on the tips. The triangular forms are the most prevalent drill types on Raccoon Notched point locations. Examples are shown in Figs. 20A–C; 17e; 23w; 25cc, dd; and 27aa. The unusual thickness and the presence of "humps" from deep-hinged terminations during thinning also suggest they were manufactured from point preform rejects.

Strike-a-Lights

Strike-a-lights are found on all Raccoon Notched point sites and are a second utilization of tip-fractured points or point rejects.

Type 1. Raccoon Side and Corner Notched Strike-a-Lights (Figs. 17f, j; 21).

General description.—These are small, side- and corner-notched points with battered distal ends.

Measurements.—Seven complete specimens show a range in length between 1.8 and 2.2 cm with an average of 2.0 cm. Width ranges from 1.6 to 2.3 cm, averaging 1.9 cm; thickness ranges from 0.4 to 0.7 cm. Stem length ranges from 0.7 to 1.2 cm, averaging 0.89 cm, and basal thickness ranges from 0.3 to 0.4 cm, averaging 0.32 cm.

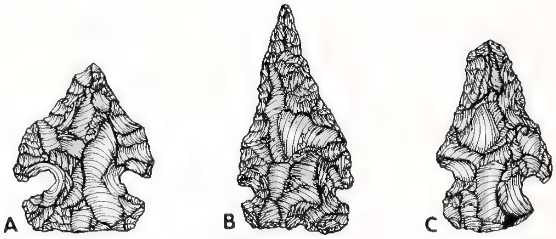

Fig. 19.—Type 3: Raccoon Side and Corner Notched Base drills: A. Onondaga, 36 WA 81; B. Onondaga, 36 WA 98; C. Onondaga, 36 WA 99.

Form.—In cross-section the notched strike-a-lights are bi-convex but occasionally are plano-convex. Edges are generally asymmetrical and excurvate to angular. The distal end is thick, rounded, and always battered. The hafting area is side- or corner-notched, with the notches of the measured specimens usually shallow, averaging 0.26 cm. The basal edge may be incurvate, straight, or occasionally excurvate and is usually thinned; some specimens are lightly ground. See Appendix I for other measurements.

Flaking.—The strike-a-lights were manufactured by the same method employed in the production of Types 1 and 2 points. The distal ends are battered, obliterating all previous primary and secondary flaking.

Remarks.—The measured sample was too small to establish the complete size range and variations within the type. It is reasonable to assume that lengths would be comparable to those of the points, but perhaps reduced through retooling. The strike-a-lights appear to be a secondary utilization of tip-fractured points or point rejects. The average thickness of the measured specimens was greater than the average of the projectile points, further suggesting that rejects were used in the production of strike-a-lights.

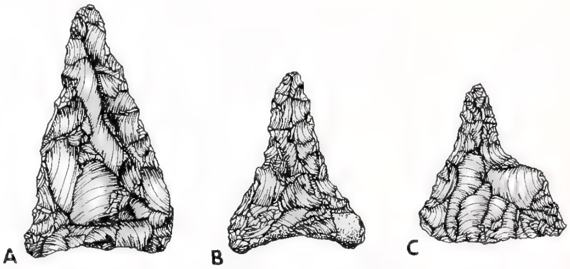

Fig. 20.—Type 4: Raccoon Triangular Base drills: A. Onondaga, 36 ER 31; B. Onondaga, 36 ER 31; C. Onondaga, 36 BV 24.

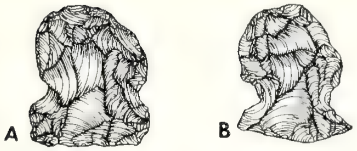

Fig. 21.—Type 1: Raccoon Side and Corner Notched strike-a-lights: A. Onondaga, 36 WA 99; B. Onondaga, 36 WA 99.

Hafted Scrapers

Hafted scrapers are found on all Raccoon Notched point sites and, like the strike-a-lights, are manufactured from tip-fractured points or point rejects.

Type 1. Raccoon Side and Corner Notched Scrapers (Figs. 17k–o, 22).

General description.—These are small, thin, side- and corner-notched points with blunt and rounded distal ends.

Measurements.—Five complete specimens provided the following measurements: length ranges from 2.0 to 2.5 cm, averaging 2.2 cm. The width ranges from 1.6 to 2.2 cm with the average being 1.9 cm. Thickness ranges from 0.4 to 0.6 cm, and stem length ranges from 0.7 to 1.1 cm, averaging 0.92 cm. The thickness of all four bases was 0.3 cm.

Form.—In cross-section the scrapers are bi-convex but occasionally are plano-convex. The distal end of the blade edge is excurvate to completely rounded, ground, and polished; and often exhibits acute flaking. The hafting area is side- or corner-notched and the depth of the notch averages 0.35 cm. The basal edge may be incurvate or straight, is occasionally excurvate and usually thinned, and most specimens are lightly ground. See Appendix I for other measurements.

Flaking.—The hafted scrapers were manufactured by the same productive techniques as point Types 1 and 2; however, the distal ends have been blunted by the removal of small finishing flakes from one or both faces, resulting in a lateral or unifacial scraping edge.

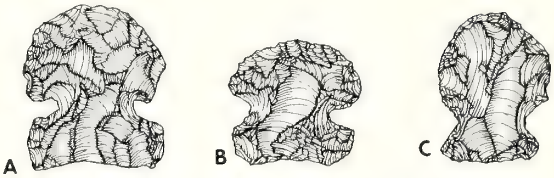

Fig. 22.—Type 1: Raccoon Side and Corner Notched scrapers. A. Onondaga, 36 BV 9; B. Onondaga, 36 BV 24; C. Onondaga, 36 WA 99.

Remarks.—The measured sample was too small to establish the complete range of sizes and variations within the type, but it is reasonable to assume that these measurements are comparable to the point types since these tools were likely made from tip-fractured points or point rejects. With the exception of the blade length, which is shorter than the average of the points, all other measurements are comparable. The most significant trait of the type is the presence of polish on the distal end of the scraper. Initially, the distal end exhibited small finishing flaking; however, continued use created polish that obliterated the flake scars. One specimen (Fig. 17o) has a graver spur.

Other Tools

Other tools not specifically described or included as part of the tool kit are pitted and unpitted hammer stones, anvil stones, pestles, and net sinkers. Some celts, pendants, a pipe, and ceramics from three major Raccoon Notched Point Assemblage sites are briefly detailed below.

OCCURRENCE OF THE ASSEMBLAGE AT THREE WESTERN PENNSYLVANIA SITES

Appendix II lists the 502 Middle Woodland sites identified during the search of the CMNH archaeological site files; 236 of these report the presence of tools from the Raccoon Notched Point Assemblage. Five sites were notable for the occurrence of the Raccoon Notched point types. Percentages for the incidence of the Raccoon Notched point types from these locations in Beaver, Warren, and Erie counties are tabulated on Table 1. In the following analysis, three of these locations, the Outdoor Theater site, 36 BV 24; the Melnick site, 36 ER 31; and the Buckaloons site, 36 WA 99, are examined. The Outdoor Theater site is located on Raccoon Creek in southwestern Pennsylvania; Melnick is situated 160 air km north on the South Branch of French Creek; and the Buckaloons site is located 64 km east of Melnick on the Allegheny River (see Fig. 1). All are situated on extensive floodplains. The evidence from these widely separated sites substantiates the concept of a Raccoon Notched Point Assemblage.

Table 1.—*Percentages for the incidence of Raccoon Notched point types from five major site locations.*

Type	Fig. no.	Site	Location	% of points/site
1. Raccoon Side Notched with excurvate blade (57% of grand total)	3, 4	Outdoor Theater 36 BV 24	Beaver Co., PA	70%
		Melnick 36 ER 31	Erie Co., PA	62%
		Buckaloons 36 WA 29	Warren Co., PA	52%
		36 WA 98		64%
		36 WA 99		50%
2. Raccoon Corner Notched with excurvate blade (22% of grand total)	5, 6	Outdoor Theater 36 BV 24	Beaver Co., PA	3%
		Melnick 36 ER 31	Erie Co., PA	25%
		Buckaloons 36 WA 29	Warren Co., PA	26%
		36 WA 98		21%
		36 WA 99		29%
3. Raccoon Pentagonal Side Notched (6% of grand total)	7, 8	Outdoor Theater 36 BV 24	Beaver Co., PA	10%
		Melnick 36 ER 31	Erie Co., PA	4%
		Buckaloons 36 WA 29	Warren Co., PA	5%
		36 WA 98		7%
		36 WA 99		8%
4. Raccoon Pentagonal Corner Notched (8% of grand total)	8, 9	Outdoor Theater 36 BV 24	Beaver Co., PA	13%
		Melnick 36 ER 31	Erie Co., PA	4%
		Buckaloons 36 WA 29	Warren Co., PA	13%
		36 WA 98		0%
		36 WA 99		6%
5. Raccoon Side and Corner Notched on Straight Blade (7% of grand total)	8, 10	Outdoor Theater 36 BV 24	Beaver Co., PA	7%
		Melnick 36 ER 31	Erie Co., PA	4%
		Buckaloons 36 WA 29	Warren Co., PA	9%
		36 WA 98		7%
		36 WA 99		8%

Without a full series of radiocarbon dates it is not possible to determine if the point types changed through time or if all the types were in continuous use throughout the postulated A.D. 500 to A.D. 950 dates for the assemblage (a summary of available radiocarbon dates follows this section). However, Ritchie's New York data for the Middle Woodland Point Peninsula Culture and its two phases, Kipp

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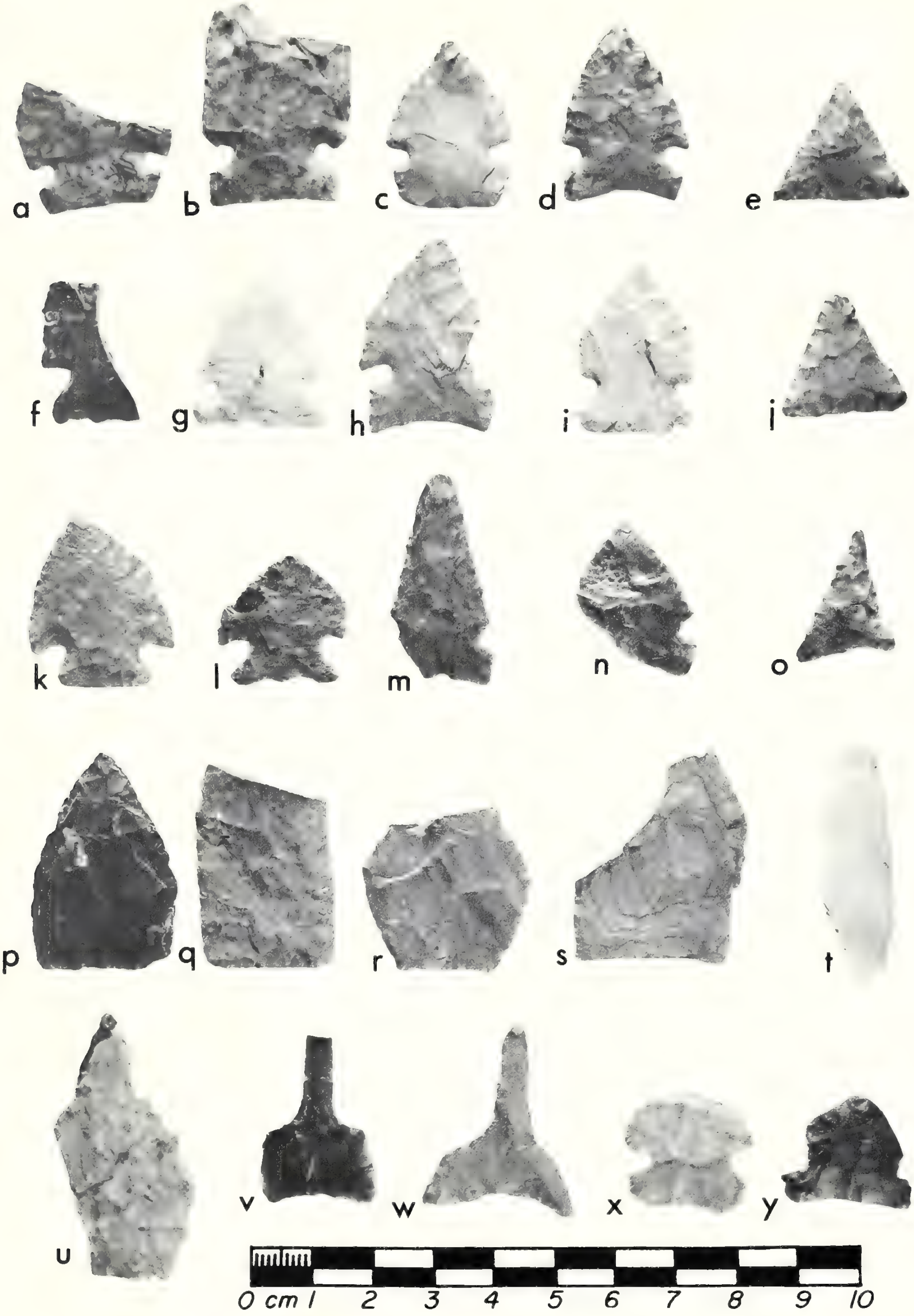
Fig. 23.—The Raccoon Notched Point Assemblage from the Outdoor Theater site, 36 BV 24. a–d. Type 1, Raccoon Side Notched points with excurvate blades; f. Type 2, Raccoon Corner Notched points with excurvate blades; g–i. Type 3, Raccoon Pentagonal Side Notched points; k, l. Type 4, Raccoon Pentagonal Corner Notched points; m, n. Type 5, Raccoon Side and Corner Notched points on straight blades; p. Type 1: Raccoon Excurvate knife; q. Type 2: Raccoon Lanceolate knife; r. Type 3: Raccoon Pentagonal knife; s. Type 4: Raccoon Corner Removed knife; u. Type 1: Raccoon Ovoid Base drill; v. Type 2: Raccoon Rectangular Base drill; w. Type 4: Raccoon Triangular Base drill; x. Type 1: Raccoon Side Notched scraper; y. Type 1: Raccoon Side Notched strike-a-light; e, j, o. Levanna points; t. Knife made on a utilized flake.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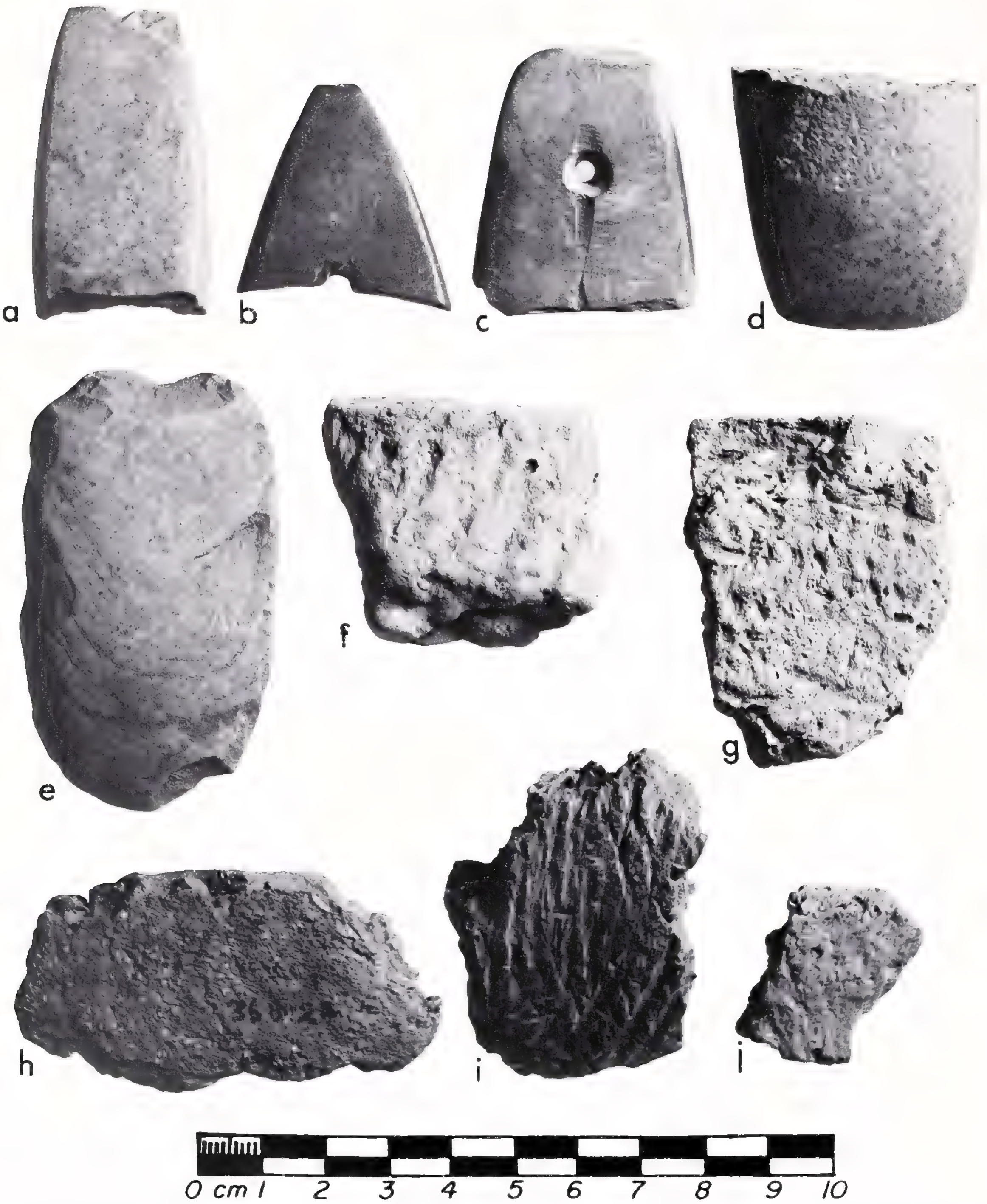

Fig. 24.—Artifacts associated with the Raccoon Notched Point Assemblage at the Outdoor Theater site, 36 BV 24. a–c. Broken stone pendants of banded slate; d, e. Celts of granite and slate; f. Rim sherd, smoothed-over, cord exterior with horizontal interior channelling and sandstone temper; g. Mahoning Cordmarked rim sherd, smoothed-over cord exterior, smooth interior with folded-down, weak collar and quartz temper; h. Rim sherd, smooth exterior and horizontally channeled interior with sandstone and quartz temper; i. Body sherd with corded exterior and smooth interior and sandstone temper; j. Watson Plain rim sherd, smooth interior and exterior with limestone tempering.

Island and Hunters Home, tend to confirm the suggested dates for the Raccoon Notched Point Assemblage.

THE OUTDOOR THEATER SITE, 36 BV 24

The type station for the distinctive Raccoon Notched points, this location has produced all of the point and tool types in the assemblage, namely, points, knives, drills, a scraper, and a strike-a-light, as well as Levanna triangular points. Another common item on Raccoon Notched point sites, a utilized flake knife, is also recorded for 36 BV 24. The tools are shown in Fig. 23; Fig. 24 contains the pendants, celts, and ceramics that accompany the point and tool assemblage. The associated Middle Woodland artifacts are similar to those identified by Ritchie from the New York White site, a Hunters Home phase occupation circa A.D. 900 ± 250 years (Ritchie, 1965:253–259). The sherds share traits with Mahoning Cordmarked (Mayer-Oakes, 1955:191) and Watson Plain ceramics (Mayer-Oakes, 1955: 195). Mahoning Cordmarked pottery was excavated in association with Raccoon Notched points at the Howard Chambers site (36 LR 3) in Lawrence County, Pennsylvania (Johnson, 1976:62).

THE MELNICK SITE, 36 ER 31

Figures 25 and 26 show Arnold Bailey's collection from this site; again, all of the Raccoon Notched point and tool types are represented, but the Type 3 Raccoon Pentagonal knives were not included in the photograph. Also unavailable for photography was a small steatite, straight-base platform pipe. All of the tools were manufactured from glacial-drift Onondaga gray and tan cherts. The Middle Woodland ceramics consist of cord malleated surfaces with applied cord decorations similar to the Point Peninsula, Kipp Island phase of New York (Ritchie, 1965:227, 232). Also represented are rims of Jack's Reef Corded and Corded Collar types (Fig. 26f, g, i) and Kipp Island Crisscross (Fig. 26j). Rocker-stamping is quite rare in northwestern Pennsylvania and western New York; however, the interior surface of one body sherd shows evidence of this technique (Fig. 26h). One corded body sherd had separated along overlapping parallel joints, suggesting that the pot was manufactured by a large coil or sectioning method (Fig. 26k).

THE BUCKALOONS SITE, 36 WA 99

While nine of the Buckaloons sites produce Raccoon Notched material, 36 WA 99, located on the floodplain of the Allegheny River, is the most extensive and prolific. Examples of the entire assemblage are represented at this site (Fig. 27). Also shown (Fig. 27dd) is a fractured, straight-based, steatite platform pipe similar to one illustrated by Ritchie (1965:256) from the terminal Middle Woodland Hunters Home phase White site in New York. The ceramics from Buckaloons are similar to those reported for the Melnick site with corded motifs over cord-roughened surfaces (Fig. 28); however, a flint tempered rim embellished with a smooth paddle edge, identified as Steamburg Tooled, is also represented (Fig. 28a). This type is considered to be Middle to Late Woodland on Allegheny Iroquois sites (Dragoo and Lantz, 1973). Other rim forms include Jack's Reef Corded, Jack's Reef Corded Collar, and Kipp Island Crisscross. Artifacts shown in Figs. 27 and 28 are from controlled surface collections made by William Stuart and John Zavinski. Some of the material has been donated and/or loaned to CMNH.

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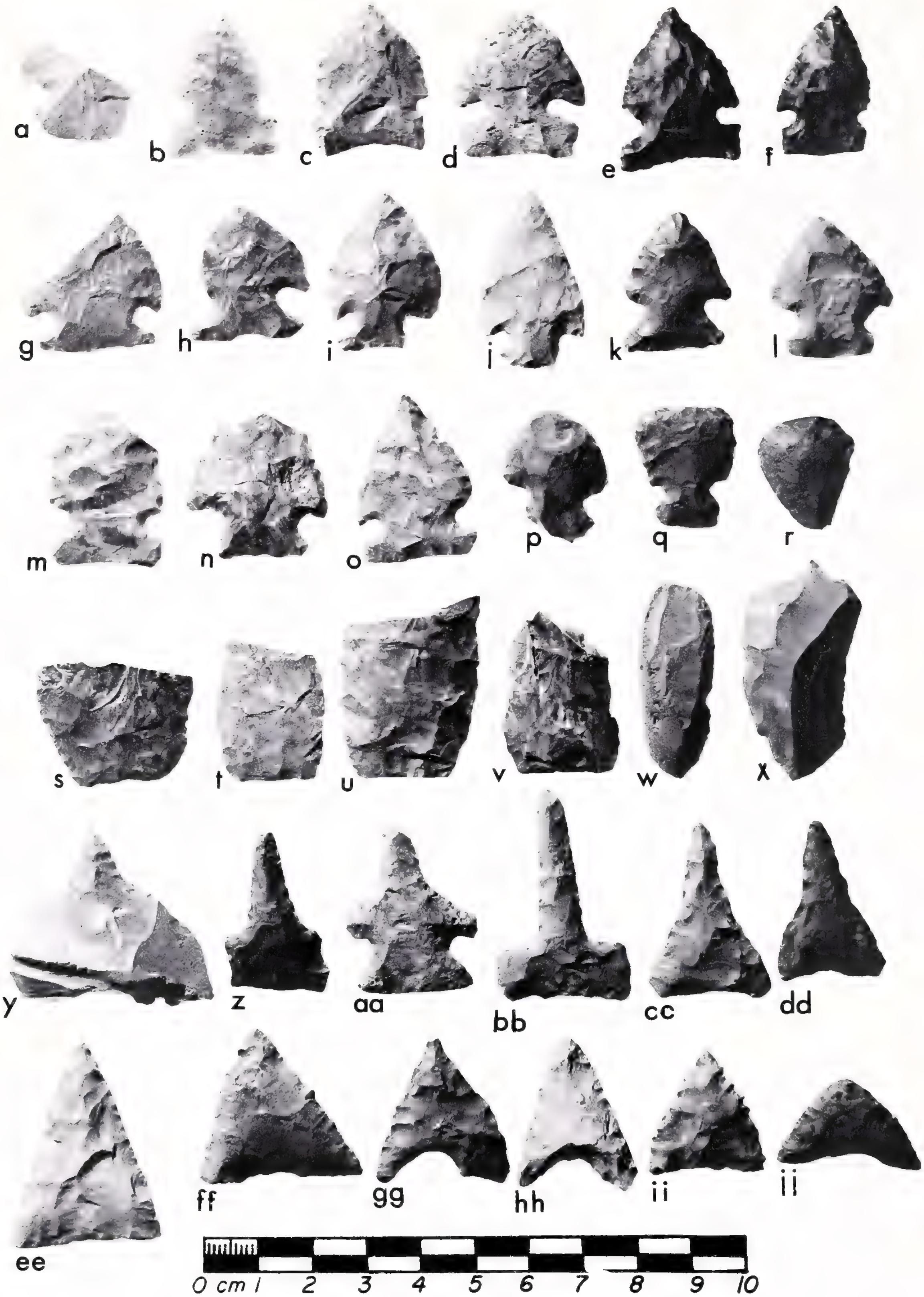
Fig. 25.—The Raccoon Notched Point Assemblage from the Melnick site, 36 ER 31. a–f. Type 1: Raccoon Side Notched points with excurvate blades; g–l. Type 2: Raccoon Corner Notched points with excurvate blades; m. Type 3: Raccoon Pentagonal Side Notched point; n. Type 4: Raccoon Pentagonal Corner Notched point; o. Type 5: Raccoon Side Notched point on a straight blade; s. Type 1: Raccoon Excurvate knife; t, u. Type 2: Raccoon Lanceolate knives; v. Type 4: Raccoon Corner Removed knife; y. Type 1: Raccoon Ovoid Case drill; z, aa. Type 3: Raccoon Side and Corner Notched Base drills; bb. Type 2: Raccoon Rectangular Base drill; cc, dd. Raccoon Triangular Base drills; p. Raccoon Corner Notched strike-a-light; q. Raccoon Side Notched scraper; r. Triangular scraper; w. Knife on a utilized flake; x. Utilized flake with spur; ee, ff, ii, jj. Levanna points; gg, hh. Extreme aberrant forms of the Waterford Triangle.

Fig. 26.—Artifacts associated with the Raccoon Notched Point Assemblage from the Melnick site, 36 ER 31. a. Slate celt; b–d. Slate pendants; e. Small grooved, quartz pebble hammerstone; f, g, i. Jack's Reef Corded and Corded Collar rim sherds; h. Body sherd with interior rocker-stamping; j. Kipp Island Crisscross rim sherd; k. Body sherd with coil breaks.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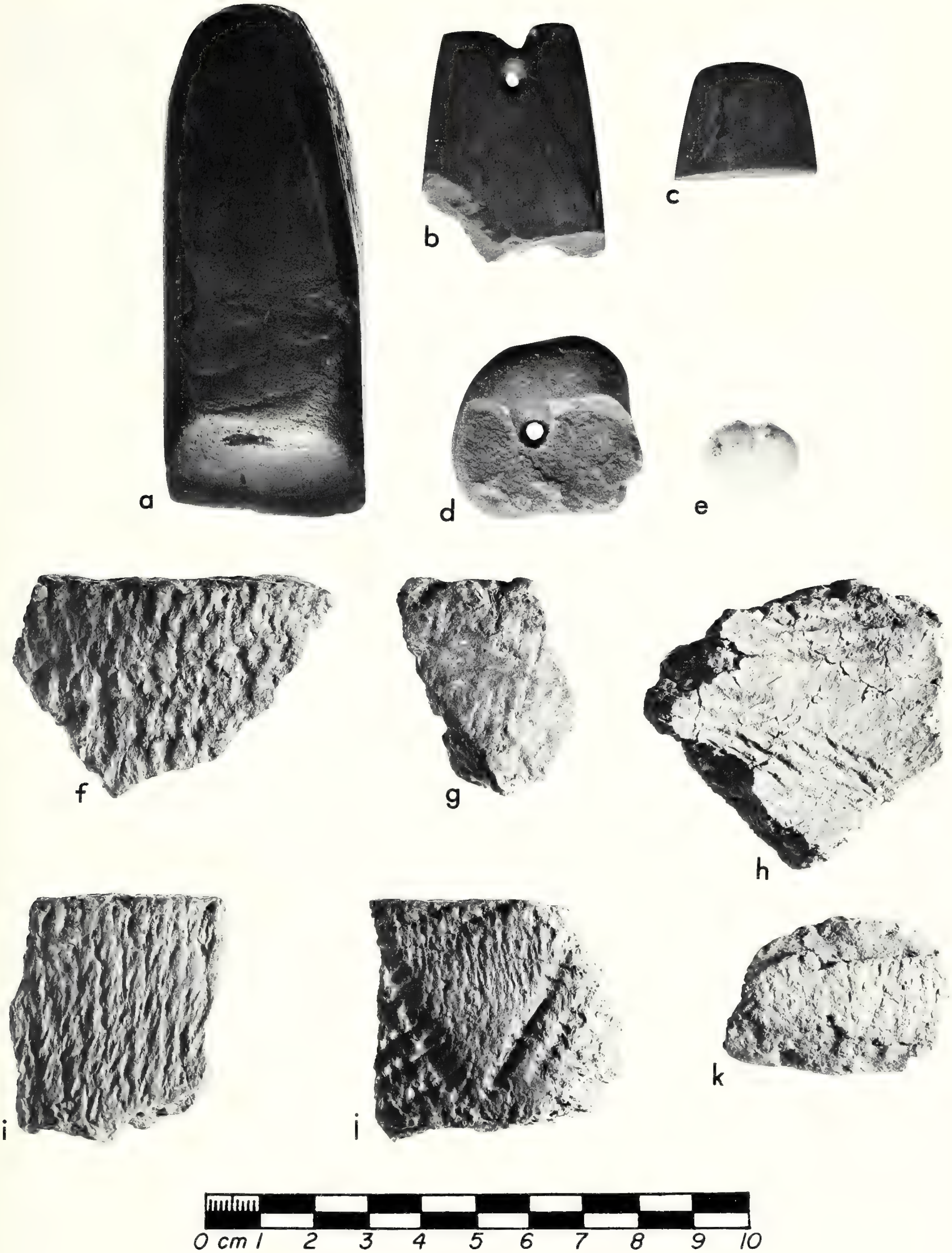
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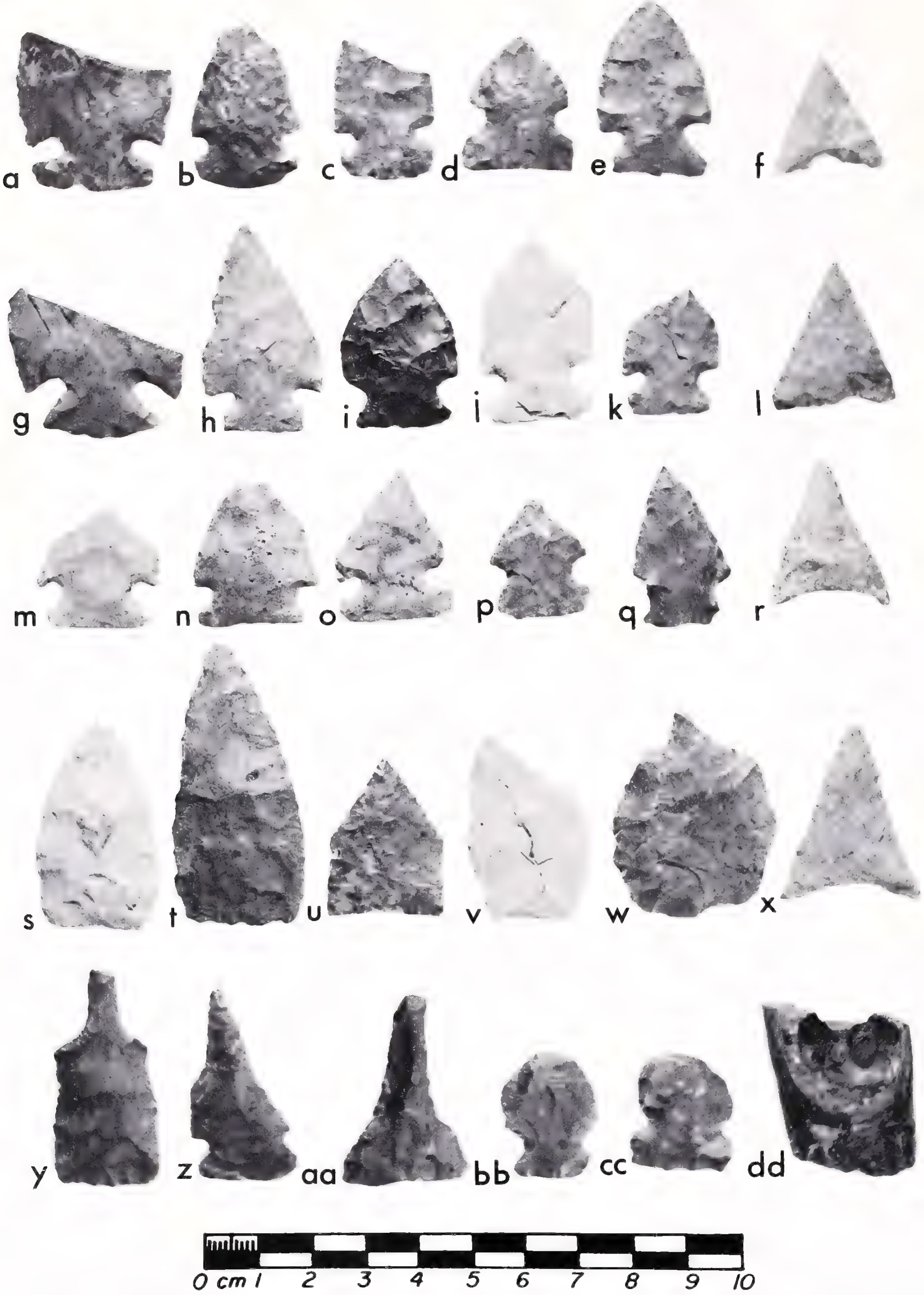

Fig. 27.—The Raccoon Notched Point Assemblage from the Buckaloons site, 36 WA 99. a–e. Type 1: Raccoon Side Notched points; g–i. Type 2: Raccoon Corner Notched points; j–k. Type 3: Raccoon Pentagonal Side Notched points; m–n. Type 4: Raccoon Pentagonal Corner Notched points; o–q. Type 5: Raccoon Corner Notched points on straight blades; s. Type 1: Raccoon Excurvate knife; t. Type

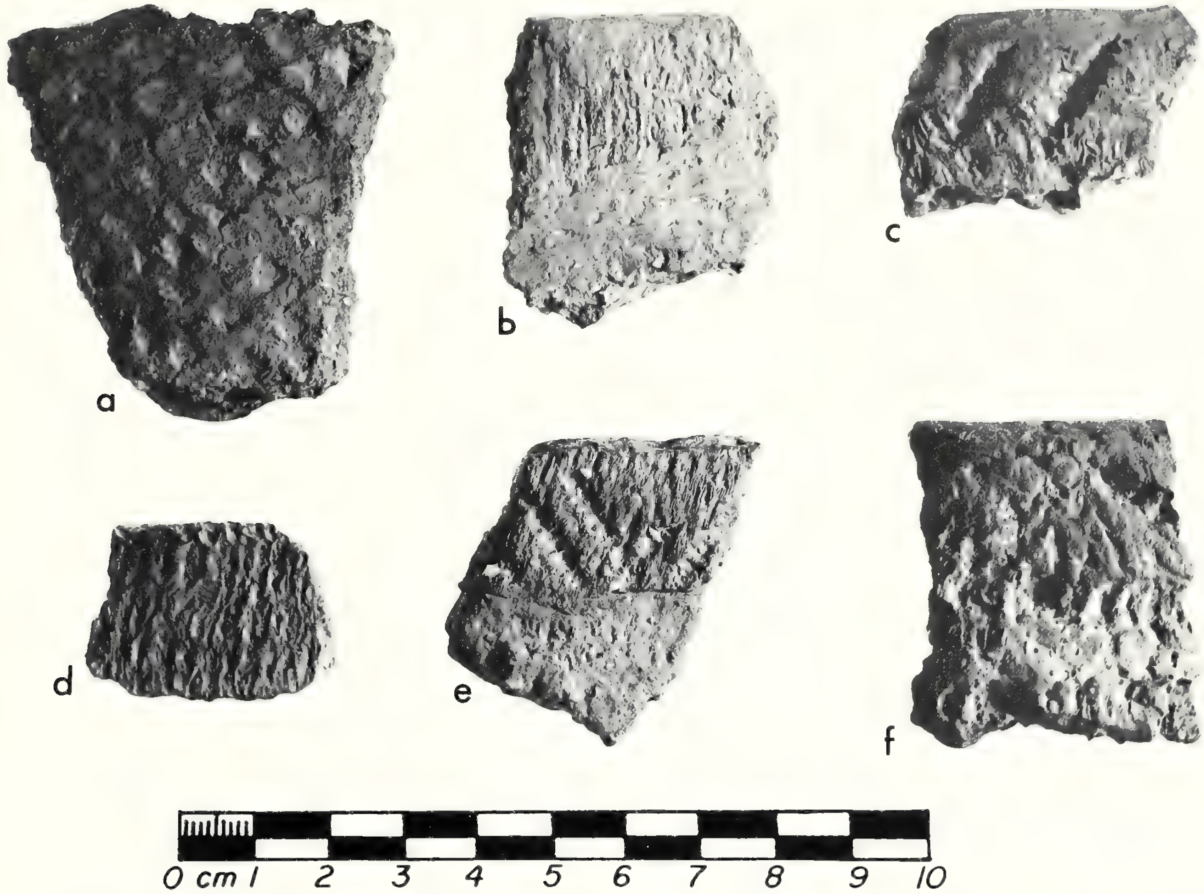

Fig. 28.—Ceramics associated with the Raccoon Notched Point Assemblage at Buckaloons sites 36 WA 99 and 36 WA 29. a. Steamburg Tooled rim sherd, flint-tempered; b, c, f. Jack's Reef Corded Collar rims; e. Kipp Island Crisscross rim sherd; d. Jack's Reef Corded rim.

SUGGESTED DATE RANGE FOR THE RACCOON NOTCHED POINT ASSEMBLAGE

The Raccoon Notched points and related tools were in use from the middle portion of the Middle Woodland period and into the initial Late Woodland. Radiocarbon dates for northwestern Pennsylvania and for the western tip of New York are well bracketed; however, the temporal range for the entire Upper Ohio Valley is less distinct. Radiocarbon dates are not available for sites located in either west central or southwestern Pennsylvania and none are reported from the portions of western New York that drain to the Upper Ohio Valley. The dates reported below, therefore, apply most directly to the northern portions of the Upper Ohio Valley in Pennsylvania.

Several radiocarbon dates obtained from Middle Woodland sites in Warren County, Pennsylvania, offer possible clues to the dates for similar forms in northwestern Pennsylvania. Excavations conducted at the multicomponent Rieder site (36 WA 103) in 1974 provided the important radiocarbon dates and established a near terminal date for the assemblage. This date came from Feature 11, a storage pit that

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2: Raccoon Lanceolate knife; u. Type 3: Raccoon Pentagonal knife; v. Type 4: Raccoon Corner Removed knife; w. Type 1: Raccoon Ovoid Base drill; y. Type 2: Raccoon Rectangular Base drill; z. Type 3: Raccoon Side Notched Base drill; aa. Type 4: Raccoon Triangular Base drill; bb. Type 1: Raccoon Corner Notched scraper with spur; cc. Type 1: Raccoon Side Notched strike-a-light; dd. Fractured bowl from steatite, straight-base platform pipe; f, l, r, x. Levanna points.

was later utilized as a refuse pit. Stratum III of the unit contained only triangular points and associated ceramics were aligned with a culture designated the Mead Island Culture. When carbon samples were submitted to Gakushuin University, Faculty of Science, Tokyo, Japan, Stratum III was dated at A.D. 1020 ± 70 years (GAK 5351). This could represent the terminal date for the assemblage since Stratum III lacks any Raccoon forms. Directly beneath, Stratum II contained a cremation burial with a Raccoon Notched point, a pentagonal knife, and a copper awl dating at A.D. 830 ± 75 years (GAK 5354). The lowest level, Stratum I, was sealed beneath and yielded dates of A.D. 390 ± 80 years (GAK 5355) and A.D. 500 ± 80 years (GAK 5353) (Lantz, 1982: 42). The lithic sample from Stratum I of Feature 11 was small and not necessarily representative of all cultural resources remaining within unexcavated portions of this site; nonetheless, Raccoon Notched materials were not present in the lowest level. Dates from Rieder bracket the Raccoon Notched Point Assemblage between A.D. 500 and A.D. 830 and terminate it by A.D. 1020. When combined with other data detailed below, the proposed date range for the Raccoon Notched Point Assemblage was established at A.D. 500 to A.D. 950.

In 1937, Mound Three (36 WA 29) of the Irvine Mound group at Buckaloons, located at the juncture of Brokenstraw Creek and the Allegheny River, was opened by Harry L. Schoff as part of his investigations of three mound sites at this location (Carpenter, 1956:89–115). Although Raccoon Notched points were recovered in quantity from sites located near the mound group, none of the distinctive tools were recovered from within the mounds (Carpenter, 1956:Plates 8, 9, 11, 16, 19). In August of 1973, CMNH excavated a five-foot test square in Mound Three and obtained a charcoal sample associated with Middle Woodland Hopewell-like materials in a deep pit. The sample was submitted to the University of Georgia Geochronology Laboratory and yielded a date of A.D. 325 ± 110 years (UGA 1642) (Lantz 1982:49).

The radiocarbon dates from Stratum III of the storage/refuse pit at Rieder and from Irvine Mound Three suggest that the Raccoon Notched Point Assemblage became an identifiable manifestation after A.D. 500; however, the tradition may have emerged much earlier in what is now New York state. Ritchie equates the Long Bay point of the early Point Peninsula, Canoe Point phase in central New York, dated at A.D. 240 ± 80 years (Y 1277) (Ritchie, 1965: 203–213), with Raccoon points. Ritchie also states that the Long Bay point was utilized into the later Point Peninsula, Kipp Island phase, and that the Long Bay point coexisted on some sites with the later Port Maitland form dated at A.D. 630 ± 100 years (Ritchie, 1971:125). The Port Maitland point is identical to varieties of Types 1 and 5 of the Raccoon Assemblage (see Figs. 3D and 10C).

Ritchie lists other similar forms and offers additional dates. The Jack's Reef Corner Notched point, although generally larger and often thicker, is very similar in morphology to the Raccoon Types 2 and 4. Ritchie reports that the Jack's Reef point was in use during the Point Peninsula 2 and 3 periods and into the early Owasco complex (Ritchie, 1971:26). The White site, a transitional site of the Hunters Home phase of the Owasco complex, was radiocarbon dated at A.D. 905 ± 200 years (M 176) (Ritchie, 1965:259, 260). Ritchie also lists the Willow Tree site in the Mohawk Valley as a probable transitional Hunters Home phase site having a radiocarbon date of A.D. 955 ± 200 years (Ritchie, 1965:260).

The Melnick site (36 ER 31) has been investigated jointly by The Carnegie and Gannon University since 1983. This location yielded a series of four radiocarbon dates to document extensive Middle Woodland components at that location and bracket approximately 300 years of prehistory. Lithic material recovered from the surface and plow zone produced items from the Raccoon Notched Point Assemblage as well as a point very similar to Ritchie's Long Bay type. Radiocarbon dates were obtained from features that survived over 40 cm of deep cultivation. Raccoon Notched points were not recovered in association with the carbon samples; however, Levanna points and variants were. One Levanna recovered in Feature 5 was dated at A.D. 525 ± 65 years (UGA 5292). Seven Levanna points, three drills, a scraper, and Jack's Reef pottery from Feature 21 were dated at A.D. 635 ± 90 years (UGA 5427). Feature 12, with a date of A.D. 690 ± 60 years, contained one Levanna point, Jack's Reef pottery, and calcined bone. Feature 10 yielded a pottery tool, calcined bone, and butternuts, and dated at A.D. 770 ± 60 years (UGA 5296). The association of Levanna points and Jack's Reef Corner Notched varieties is well documented by Ritchie (1965:243; 1971:31), who sets the date for the emergence of the Levanna point during the Kipp Island phase at around A.D. 700. This same association of triangular and Raccoon Notched points is noted in the assemblages from the Outdoor Theater, Melnick, and Buckaloons sites (see Figs. 23 to 28) and is further documented on the sites listed in Appendix II. The early date for a Levanna point at Melnick is verified by a radiocarbon date of A.D. 575 ± 180 years for a Levanna point at the Lumback site, Lorain County, Ohio (Prufer and Shane, 1976:294).

Radiocarbon dates have been obtained for Late Woodland sites in northwestern Pennsylvania and the southwestern tip of New York on sites that date diagnostics of either Proto-Iroquoian or the unpublished Mead Island Culture. These sites produce only triangular points and postdate the Raccoon Notched Point Assemblage. The cited sites, radiocarbon dates, and cultural associations are summarized in Fig. 29. The Mead Island Culture type station (36 WA 111), dated at A.D. 970 ± 75 years, is located 800 m down the Allegheny River from the Rieder site. Several recent dates for the Mead Island Culture were obtained at the Penelec site (36 WA 152) located directly across the Allegheny River from Rieder. A feature at this site containing triangular points and Mead Island ceramic types was dated A.D. 840 ± 45 years (UGA 5494). This early Penelec site date is critical since it falls within ten years of the cremation burial of A.D. 830 ± 75 years at Rieder. However, parallel and overlapping dates can be expected because of variations in material culture during periods of transition and the timing overlap of the ± factors in the radiocarbon dates. The UGA 5494 sample will be cross-checked by running an additional sample in the future. Another feature at Penelec that contained triangular points, ceramics, and bone yielded an A.D. 970 ± 45 years date (UGA 9493). An A.D. 1200 ± 70 years (GAK 5363) terminal date for Mead Island was established at the Rieder site (36 WA 103).

Charcoal from the Proto-Iroquoian Cornplanter #1 village site (36 WA 83), located 24 km upriver of the Rieder and the Buckaloons sites, was radiocarbon dated at A.D. 980 ± 100 years (M 2194). A sample from the Proto-Iroquois Vanatta site (30 CA 46), located 2 km below Salamanca, New York, near Jimmersontown, dated at A.D. 940 ± 100 years (GAK 6229). Both Cornplanter #1 and Vanatta have only triangular points in their inventories. Later excavations along this section of the Allegheny River in New York and Pennsylvania yielded radiocarbon dates that range from A.D. 1090 ± 90 years (UGA 1639) to A.D. 1525 ± 55 years (UGA 1641) (Fig. 29). No Raccoon Notched point varieties were recovered from any of these locations, all of which had extensive middens and large numbers of features.

The Upper Ohio Valley study was compared to Prufer and Shane's work in northern Ohio where the Ottawa County Libben site contained thin Jack's Reef Corner Notched points, triangular points, and some crude stemmed points, all within the traits listed for the Intrusive Mound Culture as first described by Morgan (1952:93). Three dates are given for Libben: A.D. 720 ± 105 years, A.D. 865 ± 120 years, and A.D. 955 ± 110 years (Prufer and Shane, 1976:297–300).

In summary, Raccoon Notched points were not in the inventory of Stratum I of the storage/refuse pit dating A.D. 390 ± 80 years to A.D. 500 ± 80 years at Rieder; nor were they found in the Middle Woodland Hopewell-like feature at Buckaloons that dated A.D. 325 ± 110 years. The dates of A.D. 525 ± 65 years to A.D. 770 ± 60 years at Melnick are associated with triangular points; the author assumes that these dates can be applied to Raccoon Notched points found at that site. This assumption is reinforced by the presence of Jack's Reef pottery and other dates derived from New York and Ohio. The radiocarbon date of A.D. 830 ± 75 years for the Raccoon Notched material at the Rieder site is near the terminal date for their use in northwestern Pennsylvania and southwestern New York. The Mead Island Culture with triangular points exclusively has a date range from A.D. 840 ± 45 years to A.D. 1200 ± 70 years. Triangular point Allegheny Iroquois sites, extending from Warren County, Pennsylvania, northward into Cattaraugus County, New York, are dated A.D. 940 ± 100 years to A.D. 1525 ± 55 years (Fig. 29). Taken altogether, these data indicate that the Raccoon Notched Point Assemblage dates after A.D. 500 and terminates by A.D. 950 in northwestern Pennsylvania and southwestern New York. Moreover, the Levanna point completely replaces the Raccoon Notched point in these areas before A.D. 1000.

SUBSISTENCE AND SETTLEMENT, A.D. 500–950

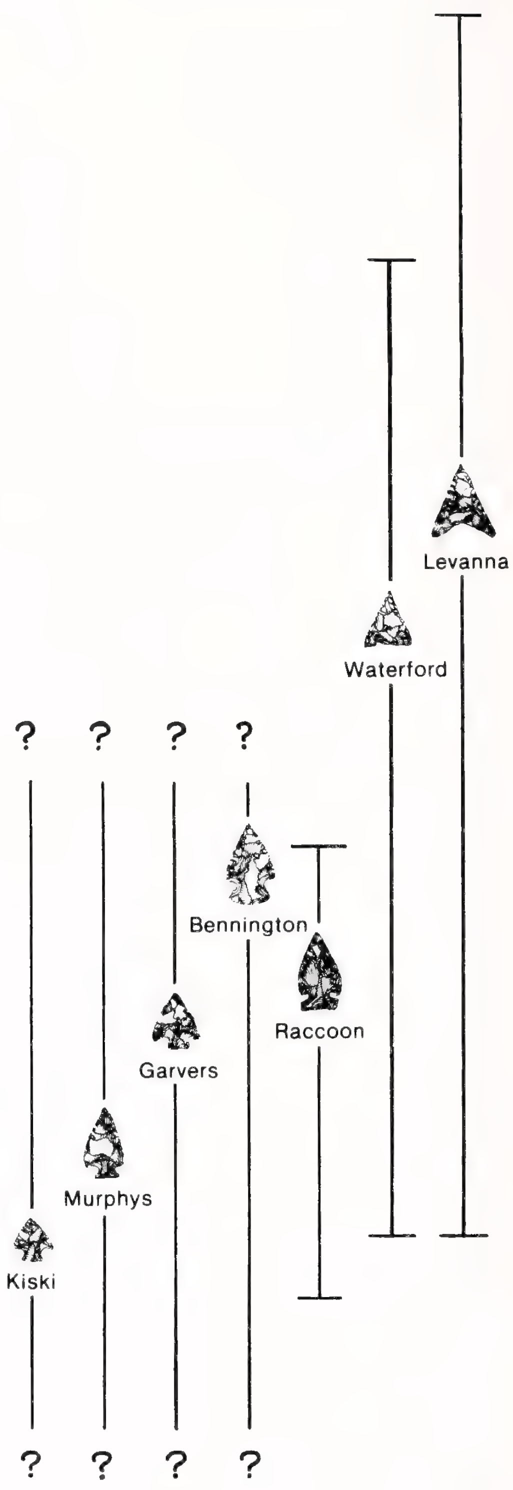
Subsistence

Many factors contributed to the abundant food resources available in the Upper Ohio Valley in western Pennsylvania and southwestern New York. Outwash from past glaciation filled valleys with glacial debris, resulting in the formation of extensive floodplain terraces (Tesmer, 1975:13; Leverett, 1934: 91–106). Before the construction of modern flood

A CHRONOLOGY OF UPPER OHIO VALLEY ALLEGHENY IROQUOIS, MEAD ISLAND, AND EARLY TO MIDDLE WOODLAND SITES.

Site No.	Site Name	Carbon 14 Date
36 WA 2	Sugar Run C.#UGA-1641	A.D. 1525 ± 55
30 CA 5	Onoville C.#M-2197	A.D. 1430 ± 100
36 WA 36	Gould C.#UGA-1640	A.D. 1340 ± 55
36 WA 84	Cornplanter 2 C.#M-2195	A.D. 1260 ± 100
36 WA 103	Rieder C.#GAK-5353	A.D. 1299 ± 70
36 CA 16	Steamburg 4 C.#UGA-1635	A.D. 1200 ± 65
36 WA 53	Kinzua C.#M-2192	A.D. 1200 ± 100
30 CA 15	Steamburg 1 C.#UGA-1634	A.D. 1145 ± 80
30 CA 35	Steamburg 2 C.#UGA-1637	A.D. 1125 ± 105
30 CA 36	Steamburg 3 C.#UGA-1639	A.D. 1090 ± 90
36 WA 103	Rieder C.#GAK-5351	A.D. 1020 ± 70
36 WA 83	Cornplanter 1 C.#M-2194	A.D. 980 ± 100
36 WA 111	Mead Island C.#GAK-5356	A.D. 970 ± 75
36 WA 152	Penelec C #UGA-9493	A.D. 970 ± 45
30 CA 46	Vanatta C.#GAK-6228	A.D. 940 ± 100
36 WA 152	Penelec C.#UGA-5494	A.D. 840 ± 45
36 WA 103	Rieder C.#GAK-5354	A.D. 830 ± 75
36 ER 31	Melnick C.#UGA-5296	A.D. 770 ± 60
36 ER 31	Melnick C.#UGA-5297	A.D. 690 ± 60
36 ER 31	Melnick C.#UGA-5427	A.D. 635 ± 90
36 ER 31	Melnick C.#UGA-5292	A.D. 525 ± 65
36 WA 103	Rieder C.#GAK-5352	A.D. 500 ± 80
36 WA 103	Rieder C.#GAK-5355	A.D. 390 ± 80
36 WA 29	Buckaloons C.#UGA-1642	A.D. 325 ± 110
36 ER 26	Wise Mound C.#UGA-5293	A.D. 160 ± 60

Point Type and Date Range



control dams, these broad valleys flooded almost annually, and the resulting overbank deposits were rich in nutrients for plant growth (Smith, 1982:16; Taylor, 1960:64–65). Streams meandered through the deposits to create oxbow lakes, abandoned channels, and occasional swampy areas (Leet and Judson, 1971:219–245). All of these environments supported a variety and abundance of floral and faunal species. The nearby forests also contributed to the subsistence base.

Ritchie's New York data (1965) and Munson et al.'s study (1971) of the Scovill site in Illinois shed some light on the probable subsistence strategies employed by Middle Woodland populations in western Pennsylvania and western New York. The Kipp Island site of the Point Peninsula 3 period was radiocarbon dated at A.D. 310 ± 100 years (Y 1378) for Kipp Island phase 2 and A.D. 630 ± 100 years (Y 1379) for Kipp Island phase 3. Ritchie (1965: 241, 242) noted that in weight, deer (*Odocoileus virginianus*) was the primary source of food; however, in total numbers, fish proved to be the most abundant with bullhead (*Ictalurus nebulosus*), channel cat (*Ictalurus punctatus*), walleyed pike (*Stizostedion vitreum*), northern pike (*Esox lucius*); bass (*Micropterus* sp.), and sucker (*Catostomus* sp.) identified. Ritchie states: "Of the 30 species of wild animals represented, 15 were aquatic. These 15 accounted for 85% of the total individual animals. Minimum number of individuals were: 56 mammals, three birds, nine turtles, six amphibians and 425 fish" (Ritchie, 1965:241). The only seeds identified from the Kipp Island excavations were carbonized goosefoot (*Chenopodium*). Ritchie theorized that horticultural products also were part of the subsistence base.

The Scovill site (Munson et al., 1971), located within the lower Spoon River valley in west central Illinois, is geographically similar to the setting of the major Middle Woodland sites of the Upper Ohio Valley. The Late Hopewellian settlement at Scovill, dated A.D. 450, demonstrates the range of floral and faunal resources available at a riverine location. The estimated food potential within a 2.87-km radius of the Scovill site is listed as follows: deer (*Odocoileus virginianus*), 103,870 kg; squirrel (*Sciurus* sp.), 24,863 kg; raccoon (*Procyon lotor*), 21,216 kg; woodchuck (*Marmota monax*), 12,376 kg; turkey (*Meleagris gallopavo*), 3,757 kg; and hickory nuts (*Carya* sp.), walnuts (*Juglans* sp.), and butternuts (*Juglans cinerea*), totaled at 864,806 hl (Munson et al., 1971:425–430). Not included in the above estimates are 27 species of fish that were recovered from pits at Scovill. The site lacked corn and beans but did produce squash (*Curcubita* sp.) and gourd (*Lagenaria* sp.). The utilization of abundant resources that were available in major river valleys has also been noted by Seeman (1979:402) and Prufer (1967*b*:316).

It is probable that the Middle Woodland populations in the Upper Ohio Valley relied heavily on the available floral and faunal resources on river terraces and in nearby catchment zones.

SETTLEMENT

Hopewell influence was extensive in the Upper Ohio Valley, especially in the upper Allegheny (Mayer-Oakes, 1955:216; Ritchie, 1965:228). Seemingly, these occupations either terminated or were culturally altered by A.D. 500. Dragoo suggested that Classic Hopewell had disappeared by that date (Dragoo, 1963:293). Review of the CMNH files and the accumulated experience of the Anthropology staff, field and regional conservation archaeologists, and collectors has made it evident that the major Hopewellian sites were utilized before and, in some cases, possibly during the emergence of the Raccoon Notched and triangular point assemblages.

Seven locations within the study area with dates that continue past A.D. 500 are especially notable for their content of Middle Woodland material; all occupy extensive terraces of up to 80 ha with large adjacent catchment zones. These are (1) Zawatski Terrace and (2) Hotchkiss Run on the Allegheny River, in Cattaraugus County, New York; (3) Sugar Run Flats and (4) Irvine Flats on the Allegheny River, in Warren County; (5) French Creek Flats in Erie County; (6) Edinburg and West Pittsburgh Terraces on the Mahoning River in Lawrence County; and (7) Raccoon Creek Terrace, Beaver County, all in Pennsylvania (Fig. 1). These locations evidence heavy concentrations of the Raccoon Notched Point Assemblage, some produce the Raccoon materials in association with triangular points, and several also have diagnostics of the Ohio Hopewell, includ-

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Fig. 29.—Chronology of point types at Allegheny Iroquois, Mead Island, and Early to Middle Woodland sites in western Pennsylvania and western New York.

ing burial mounds. These seven locations are designated as Regional Centers.

Many of the 236 sites recorded on Fig. 1 are clustered around the designated Middle Woodland Regional Centers. While many of these sites are believed to have been involved in a village removal pattern, most of the recorded associated sites were probably satellite camps utilized for hunting and gathering and for the procurement of raw materials. Undoubtedly rockshelters played an important role in the total settlement pattern, and it is unfortunate that the highly variable nature of recorded site data from these important locations prevents the inclusion of rockshelter information in this study. The clustering of sites at the Regional Center locations is obvious in Fig. 1; in all seven cases, the central locus produced evidence of intense utilization during the Middle Woodland period.

Figure 1 shows additional concentrations of Middle Woodland sites in southwestern Pennsylvania, but these are outside of the study area and, therefore, are not detailed in this publication. A notable occupation on the Ohio River in Hancock County, West Virginia, at the Watson site (46 HK 34) where extensive Early to Middle Woodland occupations and a series of mounds are documented, certainly qualifies as a Regional Center but it also is outside of the study area.

The large Regional Center terraces in northwestern Pennsylvania and western New York were not totally occupied at any given time; however, a settlement system of village movement was taking place throughout Middle Woodland times, from 100 B.C. to A.D. 900. Each village was used for a period of time before exhaustion of firewood, rotting of house structures, flooding, and—to a lesser extent—soil depletion, necessitated a move to a new location, to a valley terrace several miles distant. Eventually each village returned to its original location or an adjacent one. This same village removal pattern continued in Late Woodland times as exemplified by the Allegheny Iroquois (Dragoo and Lantz, 1975:82). The village return pattern resulted in quantities of occupational debris being scattered over an expansive area—up to 9 sq ha at the Melnick sites (36 ER 31 and C-36 ER 181), where Middle Woodland occupations date between A.D. 500 and A.D. 800.

An excellent example of continued reoccupation is found at the Irvine Flats on the Allegheny River below Warren, Pennsylvania. Raccoon Notched and triangular points can be found on nine recorded sites on that 101.2 ha terrace and two large areas have concentrations of these assemblages; however, six others show extensive Hopewellian-like occupations, including nine burial mounds on or near the flat (Lantz, 1982:40; Lantz et al., 1982:48, 49). Some of these mounds were reported and described by Carpenter (1956:89–112).

A brief review of specific geographic areas within river valleys where major Regional Centers appear to have been associated with ancillary sites follows.

Zawatski Terrace

During a 1976 survey, limited test excavations and controlled surface collections were conducted at 27 archaeological sites located on the extensive Zawatski Terrace on the Allegheny River at the confluence of Great Valley Creek near Killbuck, Cattaraugus County, New York (Figs. 1 and 30). Artifacts recovered from the extensive work at Zawatski Terrace are curated at the Division of Anthropology, CMNH. Three sites, C-30 CA 70, C-30 CA 74, and C-30 CA 93, with Late Point Peninsula ceramics are believed to represent the terminal period of the Raccoon Notched/triangular point association, dating from circa A.D. 800 to A.D. 950 (Dragoo et al., 1976).

The most recent village of the Zawatski group may have been relocated several miles downriver below Salamanca, New York, on what is called Hoags Flats. At Hoags Flats, the Vanatta site (C-30 CA 46) was excavated in 1972 (Lantz, 1974:83–86) and contained ceramics similar to Wickham Punctate and the Princess Point complex of southwestern Ontario (Ritchie and MacNeish, 1949:105; Stothers, 1976: 151) and triangular points exclusively. Vanatta was dated at A.D. 940 ± 100 years (GAK 6229). Another Hoags Flats location with triangular points and Wickham Punctate pottery was excavated in 1969 by Liddell and Henke of the State University of New York at Buffalo. This site was thought to date around A.D. 1000 (Liddell and Henke, 1969:18). The settlement pattern of village relocation evidently continued with a reoccupation of a large area of the Zawatski Terrace. Sites C-30 CA 71 and C-30 CA 72 were Late Woodland sites containing triangular points and Allegheny Iroquois varieties of exterior cordmarked rims and sherds.

That the Zawatski Terrace was important during early Middle Woodland times is supported by the presence of the Killbuck Mound (C-30 CA 73) and other sites that produce Middle Woodland materials. Sites located near the mound, C-30 CA 75 and C-30 CA 76, produced a Snyders point of an un-

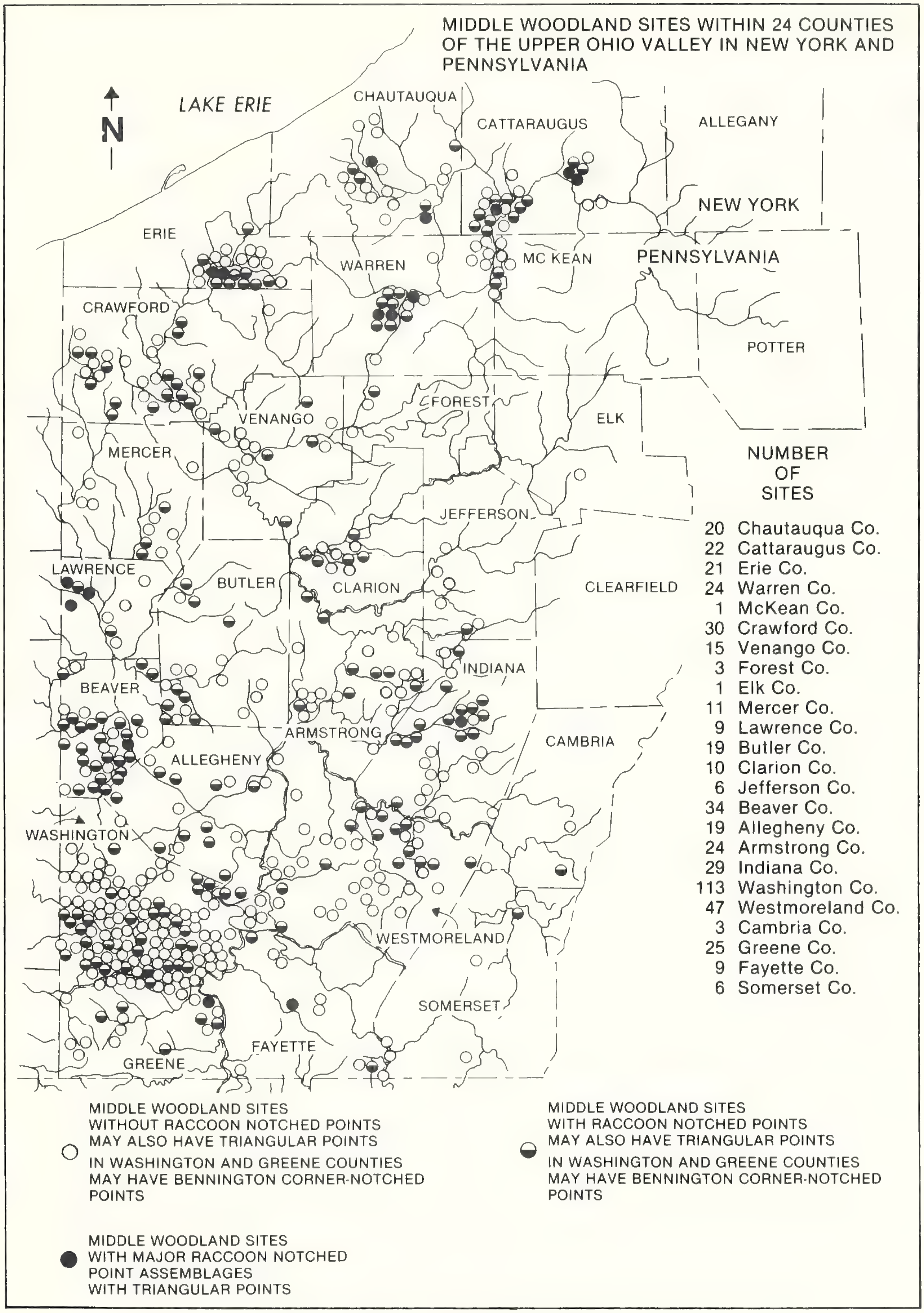

Fig. 30.—Distribution of Middle Woodland sites with Raccoon Notched and triangular points.

known exotic gray flint, Middle Woodland cache blades of Onondaga chert, and artifacts made from Ohio chalcedony. The Killbuck Mound may have been first excavated by Melvin Fillmore in 1893 and again by King Tanty Jimerson in 1920 (Carpenter, 1950:247–249). An outstanding curved-base monitor pipe, reported as being from a mound at Killbuck, is classic for Hopewell (Hart, 1975:18, 19). The Killbuck Mound was re-excavated by Carpenter in 1949 when cache blades, gorgets, copper artifacts, and a point were recovered. Parker and Carpenter reported six more mounds near Vandalia, New York, upriver from the Zawatski Terrace (Parker, 1920: 498–500; Carpenter, 1950:249–255). Ritchie (1965: 213–215) refers to the Killbuck and Vandalia mounds as being within the Squawkie Hill phase, a northeastern Hopewellian cultural expression.

Little survey or testing has been done along the major terraces upriver of Killbuck and it is possible that a number of major, but yet unrecorded, Middle Woodland sites may be located there. The recorded information at hand indicates that a number of related Middle Woodland sites are clustered around the Zawatski Terrace.

Hotchkiss Run

The Hotchkiss Run site (C-36 CA 25) is another Cattaraugus County, New York, site which may have served as a Regional Center. This extensive site, now destroyed by the construction of the Allegheny Reservoir and erosion following the completion of the reservoir, was located on the Allegheny River 1.9 km above the Pennsylvania/New York state line. As illustrated in Figs. 1 and 30, a cluster of Middle Woodland Raccoon Notched point sites surround the location. Hotchkiss Run is estimated to date during the Kipp Island phase 3 of Point Peninsula (Ritchie, 1965:228; Ritchie and Funk, 1973:155). All Raccoon Notched and triangular points from this location are manufactured from varieties of Onondaga chert. Included in surface collections are flake knives and projectile points of Flint Ridge chalcedony. An unusually large triangular tool from Hotchkiss Run is shown in Fig. 31k (Dragoo and Lantz, 1969:45–49).

Near Hotchkiss Run, along the Allegheny River, were several sites that collectively span the full range of Middle Woodland. These sites, all of which had burial mounds in association, included Cold Spring I and II (C-30 CA 12, C-30 CA 10) (Parker, 1920: 498; Lantz, 1971:13–15), Sawmill Run (C-30 CA 30), Sawmill Run South (C-30 CA 100), and the Mound site (C-30 CA 67) (Parker, 1920:498). Included in the surface collections from these sites are flake knives and projectile points of Flint Ridge chalcedony and Raccoon Notched points. The materials from these sites, as well as from the Hotchkiss Run site, were documented in the collections of Lyn Beach, Robert Orth, William Stuart, John and Jim Zavinski and others.

Sugar Run Flats

Another important complex of Middle Woodland sites was located 19 km above Warren, Pennsylvania, on the Allegheny River and, like the Hotchkiss Run location, is now inundated by the Allegheny Reservoir. Sites affiliated with the Sugar Run Flats are shown in Figs. 1 and 30. Seven kilometers upriver, Carpenter reported five mounds on the Cornplanter Grant (Carpenter, 1950:241–243). Ritchie (1965:214) referred to this section of the Allegheny River as a regional center of Hopewellian traits.

The sites with strong Hopewellian traits extend from the Berkabile #1 site (36 WA 15) north to the Langler Mound (36 WA 24), a distance of several kilometers. Other than a mention in Carpenter's notes (CMNH files) of a mound being in the area, and the discovery of a mound base and a mass of red ochre by Lantz in 1960, there is no information available for Langler Mound. Central to this extensive river terrace were the famous Sugar Run Mounds and village (36 WA 2). The mounds were excavated by Carpenter and Wesley L. Bliss in 1941, and a section of the village north of the mound was investigated by Shirley Bliss under the supervision of her husband (Carpenter, 1950:184–240). A more-northern section of the village area was excavated during 1964–1965 by the Kinzua Chapter No. 18 of the Society for Pennsylvania Archaeology. Afterwards this material was photographed and some of the artifacts were donated to CMNH.

The Sugar Run village produced a quantity of Middle Woodland flake knives and Chesser Notched points of Flint Ridge chalcedony, Raccoon Notched points, and several flakes of obsidian. The mounds produced eight gorgets, fifty-one chert and three jasper cache blades, one chert knife and one chalcedony flake knife, four fragments of sheet muscovite, one oval piece of sheet mica, one galena crystal, one copper awl, one piece of sheet copper, three chert projectile points, three bear canines, one turtle carapace, one deer antler, Illinois Hopewell-like decorative pottery, red and yellow ochre, and other items (Carpenter, 1950:189–203).

A bulldozer cut was made 152 m north of Sugar Run in 1965, exposing several pits that were recorded as site 36 WA 133. Several flake knives of chalcedony were recovered in association with some unusually hard, untyped, Middle Woodland pottery. The vessels were fairly large with expanded flat lips, fine smoothed-over cord exteriors with horizontal fabric impressions on the interior of one, and random cording on the interior of another (Lantz, 1971: 12).

The nearby Berkabile site (36 WA 15) also contained a Middle Woodland component. Flake knives and points of Flint Ridge chalcedony and gorget fragments are in the CMNH collections. A small mound that had been plowed down by 1961 was reported by Mr. Fuller of Kinzua, Pennsylvania, as being east of PA Route 59 on the edge of an old overflow channel on Berkabile property. In the Fuller collection were several Flint ridge blades reported as having been found there and stone slabs and several flake knives were found at the location. Mr. Berkabile believed that the stone used in the construction of his tool shed had come from the field and, based on the accumulated evidence, the location was recorded as the Berkabile Mound (C-36 WA 235).

During the Dragoo and Ritchie Allegheny Reservoir survey in 1958 the following Middle Woodland sites were recorded within several kilometers of the Sugar Run Mounds: 36 WA 7, 10, 12–15, 17, 19–21, and 24. Another recently recorded mound, C-36 WA 231, was first reported in 1965 during construction of the Kinzua Beach Park. Workmen reported finding large blades, a gorget, and a pipe. Erosion has recently exposed additional Flint Ridge flake knives and cache blades that are now in the John Zavinski collection.

In October of 1986, a slab rock burial mound (C-36 MC 14) was discovered by Zavinski and the author in McKean County during a survey of Nelse Run. Nelse Run enters Sugar Run 1.2 km east of the Sugar Run Mound. This newly discovered mound, also under the summer pool of the reservoir, was exposed by erosion. Other than calcined bone and flint flakes recovered in the mud, no artifacts remained and a large capstone had been removed by persons unknown.

Ritchie established the Squawkie Hill phase of Middle Woodland, a manifestation comprised of the possible merging of local cultures and that of the intrusive Hopewell; in western Pennsylvania he includes the Sugar Run mounds and mounds downriver at Irvine as components of the Squawkie Hill phase (Ritchie, 1965:214, 215).

Irvine Flats (Buckaloons)

Irvine Flats is a significant 101.2 ha terrace located on the Allegheny River adjacent to the mouth of Brokenstraw Creek 8.5 km below Warren, Pennsylvania (Figs. 1 and 30). The major Middle Woodland occupation has many Hopewellian attributes. Artifacts of exotic lithics and distinctive imported items have been recorded in quantity from the Buckaloons sites. Projectile point types included Manker Stemmed, Manker Corner Notched, Chesser Notched, and Snyders points manufactured from Flint Ridge, Plum Run, and Coshocton, Ohio, lithics. Occasionally Onondaga cherts from Pennsylvania glacial outwashes were utilized. Of the ten recorded Middle Woodland sites on the Irvine Flats (Fig. 1), Raccoon Notched Point Assemblage materials have been recovered from nine: 36 WA 29, 31, 93, 95, 96, 97, 98, 99, and 102. The various point and tool types from these locations are illustrated in Figs. 3 through 22 and are listed in Appendix I. Representative points and tools from the Raccoon Notched Point Assemblage from 36 WA 99 are shown on Fig. 27 and listed in Appendix II. Ceramics from 36 WA 29 and 99 are illustrated on Fig. 28.

Hopewellian-like materials are concentrated on sites 36 WA 29, 30, 31, 95, 96, 97, and 98. The collections at CMNH from these sites include Chesser, Manker, and Snyder points; prismatic flake knives; Middle Woodland ceramics; and various tools. Deep cultivation of 36 WA 97 in 1978 exposed a small feature containing ceramics, a Flint Ridge cache blade (Fig. 32b), and a waste flake of chalcedony. A ceramic rim sherd, quartz and sandstone-tempered with oblique dentate stamping (Fig. 32a), was also recovered. The rim is similar to pottery from the Donaldson site of the Saugeen focus of Ontario (Wright and Anderson, 1963:49, Plate 13) and appears to be related to the Early Point Peninsula Culture of New York (Ritchie, 1965:205) and Vinette Dentate ceramics (Ritchie and MacNeish, 1949:101).

Affiliated with the Irvine Flats Regional Center are several of the Harrington Farm sites, located across the Allegheny River. In 1972, a small section of the Herrington Farm #2 site (36 WA 87) was salvaged and a large pit was exposed. It contained

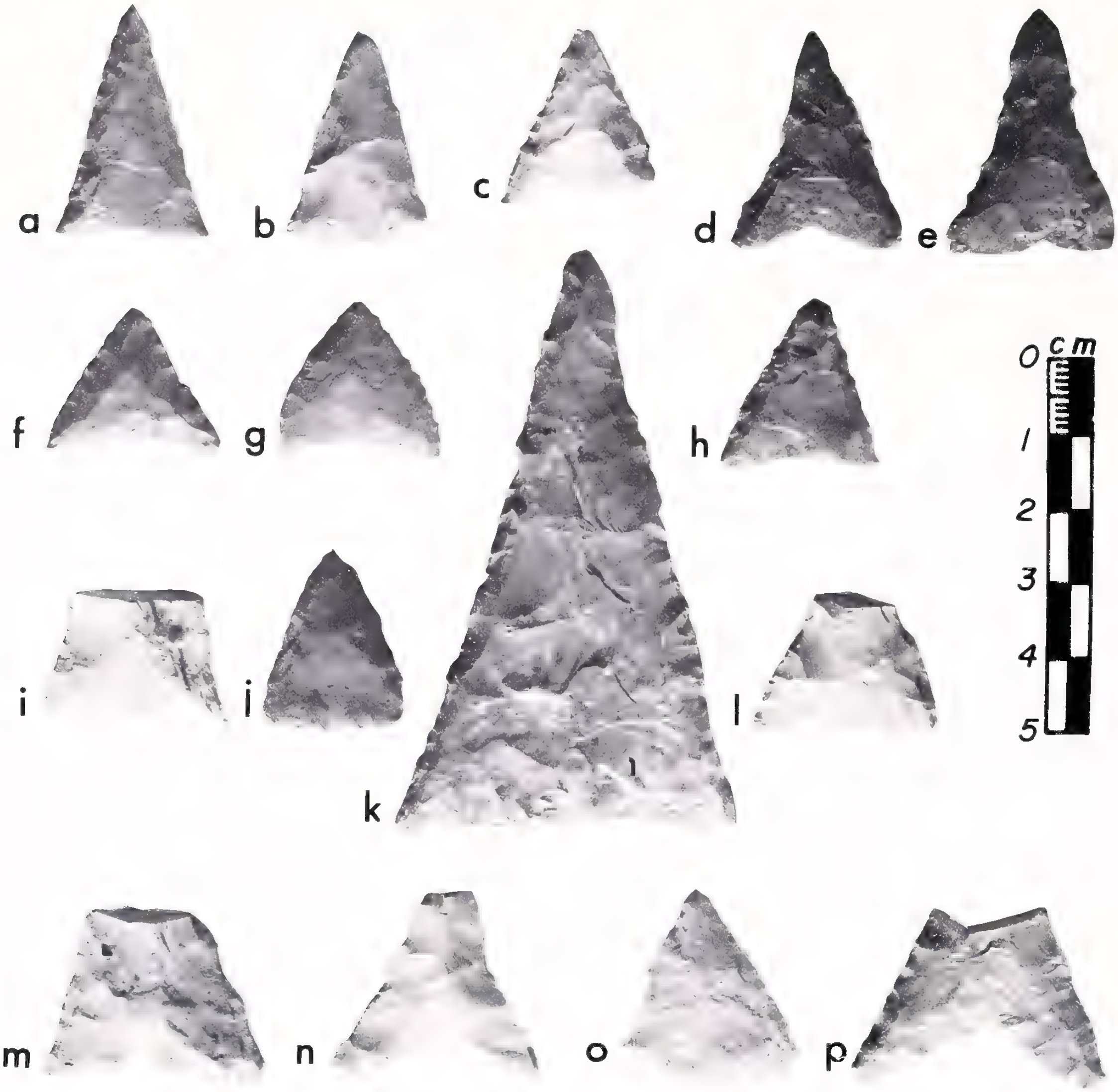

Fig. 31.—Levanna and Waterford triangular points from the Melnick site, 36 ER 31; large triangle from the Hotchkiss Run site, 30 CA 25. a. Waterford, Onondaga, 36 ER 31; b. Levanna, Delaware, 36 ER 31; c. Levanna, Delaware, 36 ER 31; d. Levanna, Onondaga, 36 ER 31; e. Waterford, Onondaga, 36 ER 31; f. Levanna, Onondaga, 36 ER 31; g. Levanna, Onondaga, 36 ER 31; h. Levanna, Onondaga, 36 ER 31; i. Waterford, Delaware, 36 ER 31; j. Levanna, Onondaga, 36 ER 31; k. Levanna, Onondaga, 30 CA 25; l. Waterford, Delaware, 36 ER 31; m. Waterford, Delaware, 36 ER 31; n. Levanna, Delaware, 36 ER 31; o. Levanna, Delaware, 36 ER 31; p. Levanna, Delaware, 36 ER 31.

flake knives, scrapers, a Steuben point, a point base that is possibly from a Snyders point, and Hopewell ceramics. In Fig. 33e, the large broken blade is manufactured from Coshocton, Ohio Upper Mercer flint as is the spurred scraper (f). The Steuben point (g) is Onondaga chert whereas the possible Snyders point base (h) is manufactured from Flint Ridge chalcedony. The ceramics include one rim sherd (Fig. 33a) that is most similar to Point Peninsula Plain (Ritchie and MacNeish, 1949:103). The feature also contained dentate stamped rim and neck sherds with a herringbone design (Fig. 33c, d) most similar to Central Illinois Valley Hopewell (Wray, 1952: Figs. 73, 74). There are resemblances to ceramics from the Middle Woodland Winooski site near Lake Champlain in northwestern Vermont (Petersen and Power, 1983:119, 160) and the Pseudo Scallop Shell rims from the Donaldson site in Ontario (Wright and Anderson, 1963:Plate XI, 6). Another rim (Fig. 33b) has some resemblance to Tittabassee Ware vessels from the Schultz site, Saginaw County, Michigan, that was radiocarbon dated between A.D. 1 and

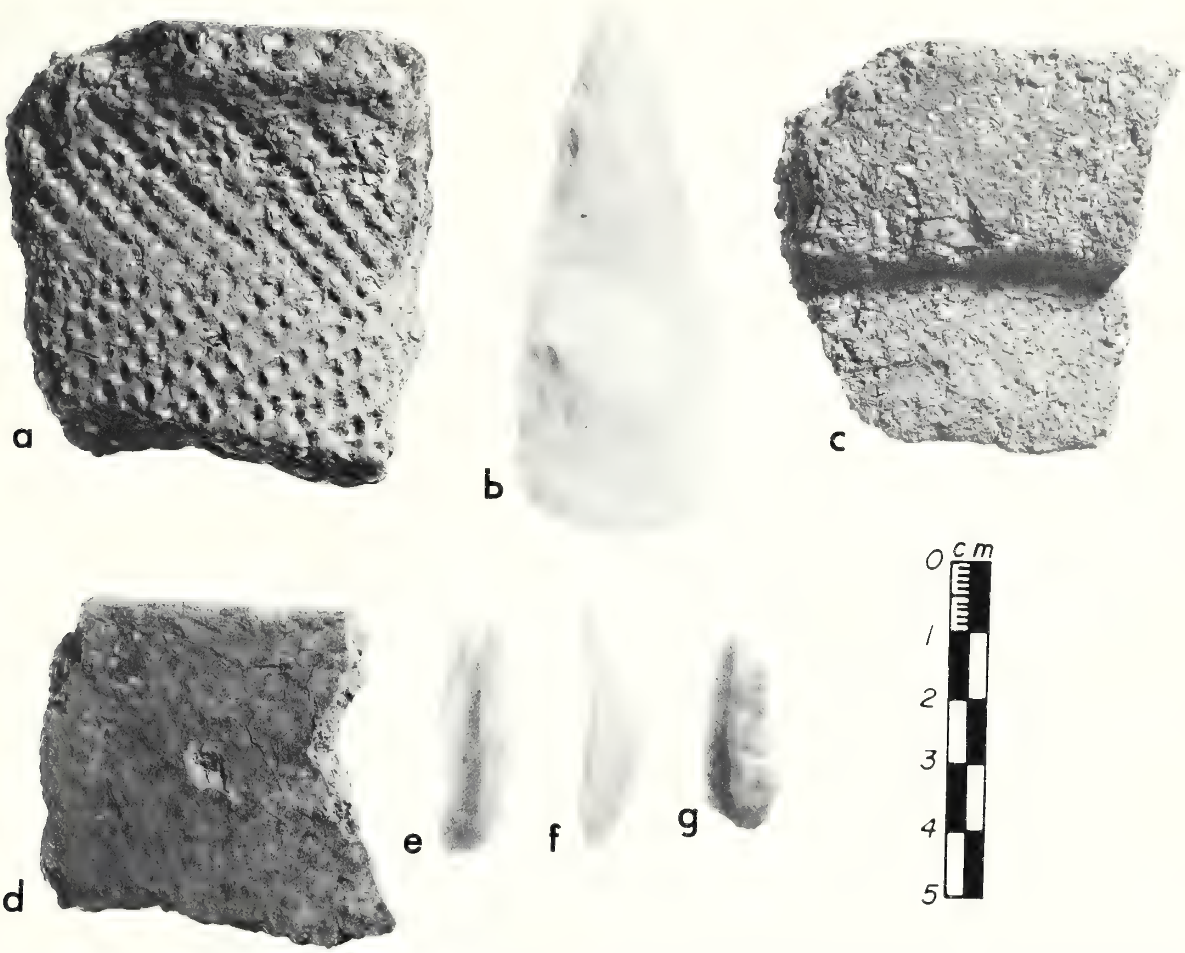

Fig. 32.—Middle Woodland artifacts from the contents of two features at Buckaloons sites 36 WA 29 and 36 WA 97. a. Dentate stamped rim sherd, herringbone pattern, quartz and sandstone temper, 36 WA 97; b. Triangular biface, Flint Ridge chalcedony, 36 WA 97; c. Plain-collared rim, quartz and sandstone temper, 36 WA 29; d. Rim, smooth exterior with horizontal corded interior and flat lip, quartz and sandstone temper from 36 WA 29 found in association with c, e, f, and g; e–g. Prismatic flake knives, Flint Ridge chalcedony, 36 WA 29.

A.D. 300 (Fitting, 1972:153–155, 257). The Harrington specimen is unusual, with spaced vertical stamping that suddenly closes to form triangles. The lip also has oblique dentate stamping while the sublip appears to have been rocker-stamped.

Under an agreement with the National Forge Company, CMNH had exclusive access for surface collecting at Irvine Flats (Buckaloons) for a period of five years. This arrangement with National Forge resulted in the procurement of provenienced artifacts and extensive collections of materials. During this time, 17,000 artifacts were amassed by CMNH regional conservation archaeologists William Stuart and John Zavinski. A small private grant from Stuart enabled CMNH to conduct some test excavations and obtain a radiocarbon date of A.D. 325 ± 110 years (UGA 1642) for Mound Three of the Irvine group (Lantz, 1982:40).

Numerous exotic prismatic flake knives, fragments of sheet mica, and recently an unusual mica gorget have been collected from plowed fields near the mounds. The Stuart and Zavinski collections contain 26 complete and fragmentary prismatic chalcedony knives from the area around Mound One.

Mounds One and Two were first explored by Roscoe D. Ransom in 1885. These mounds, as well as Mounds Three and Five, were investigated in 1937 by Harry J. Schoff. With the exception of Mounds Three and Five, the reopened mounds contained

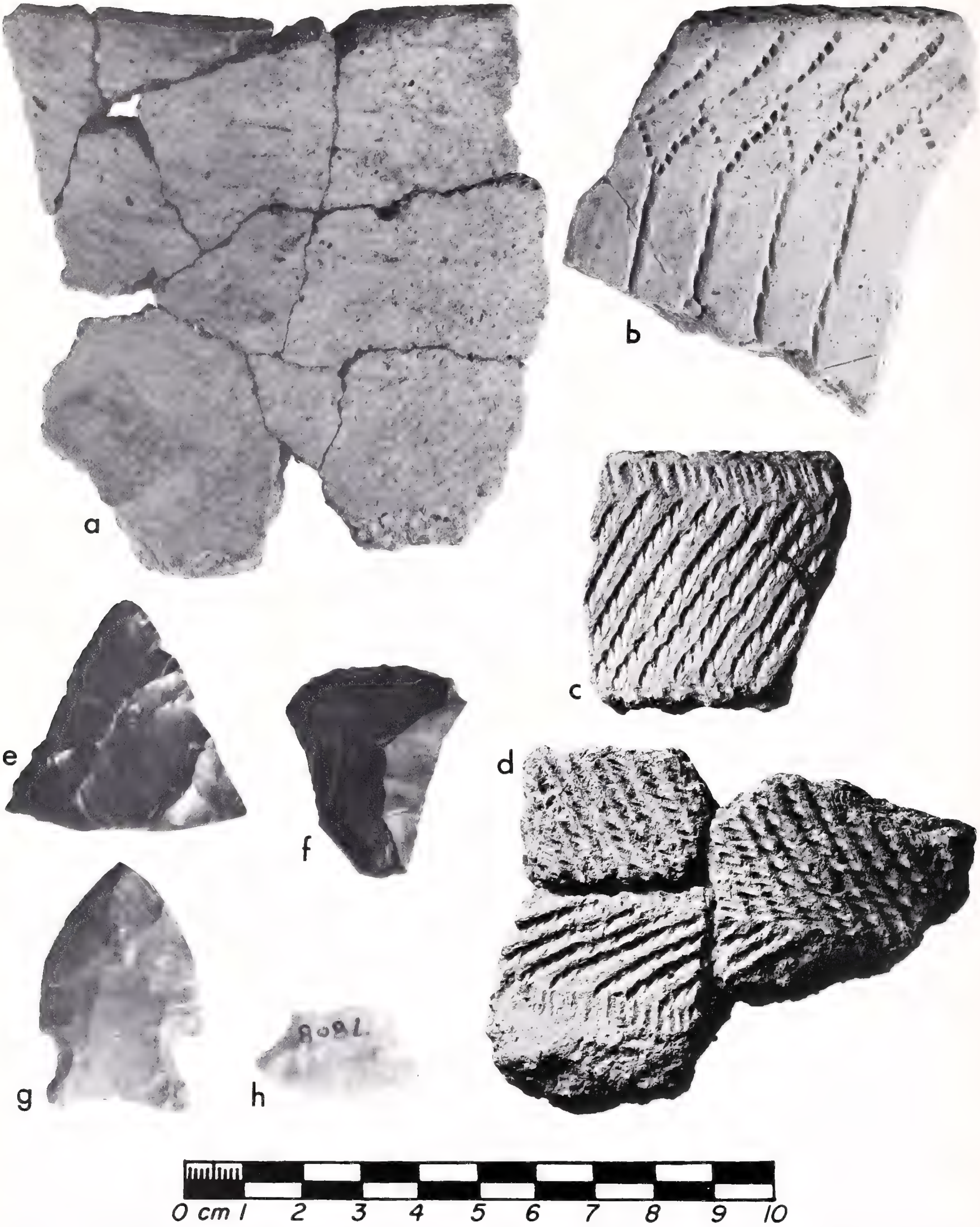

Fig. 33.—Middle Woodland artifacts from a feature at the Harrington Farm, 36 WA 87. a. Point Peninsula Plain rim sherd; b. Rim sherd, similar to Tittabassee Ware vessels from the Shultz site, Saginaw County, Michigan; c, d. Rim and neck sherds from one vessel,

exotic materials including native silver, sheet copper, a clay platform pipe, and a stone hemisphere (Carpenter, 1956:151–183). In 1973, CMNH excavated a test square in Mound Three (36 WA 29) and encountered a feature that contained three chalcedony flake knives (Fig. 32e, f, g), sheet mica, red ochre fragments, chalcedony and Onondaga chert flakes, miscellaneous lithic materials, and 44 grit-tempered sherds and rims. Three types of pottery were present: sherds with smooth exteriors and horizontally corded interiors, sherds with corded exteriors and smooth interiors, and sherds with smooth exteriors and interiors. Rim sherds from the sample generally have flat lips with smoothed exteriors and horizontally corded interiors (Fig. 32d). One sherd with a rounded lip, flat collar, smooth exterior, and a horizontally corded interior was also recovered (Fig. 32c). The plain-collared ware was previously unknown for western Pennsylvania. Its counterpart is in the Adena to the southwest in Ohio, Kentucky, and southeastern Indiana (Morgan, 1952:86, Fig. 31A). However, at Buckaloons, Adena blades were neither associated in the feature nor recovered from the plowed fields in the immediate area of the mound. The uncollared ware from the excavated feature near Mound Three was comparable to the rim sherds excavated from Mound One by Schoff (Carpenter, 1956:107).

Sites at the Irvine Flats have been occupied intermittently since Paleo Indian times. An assessment of the collected cultural material suggests that occupation there covered the span of Middle Woodland. Analysis of the lithics shows a separation of flint types utilized during Middle Woodland Hopewell—or prior to A.D. 500—and those used by groups producing the Raccoon Notched Point Assemblage after A.D. 500. The Hopewell inventory is comprised of 755 items of Flint Ridge chalcedony, 30 Coshocton, 9 Plum Run, 6 Skyhill, and 258 from Onondaga chert. Ohio lithic sources accounted for 75% of the total. In contrast, the Raccoon Notched Point Assemblage inventory lists 215 items of local Onondaga cherts and just five items produced of Coshocton, Ohio, flint or only 2.3%. This shift in lithic procurement is also evidenced at the Melnick site (36 ER 31) where the Raccoon materials have only 2% Ohio-sourced lithics. Thus, at two of the Regional Centers, Irvine Flats and French Creek, almost all movement of Ohio lithic sources ceases around A.D. 500.

French Creek Flats

Middle Woodland Melnick sites 36 ER 31 and 36 ER 181 are the nuclei of the Regional Center on the French Creek Flats. They are located several kilometers southeast of Waterford, Pennsylvania, within a meander on the South Branch of French Creek. Radiocarbon dates at 36 ER 31 range from A.D. 525 ± 65 years (UGA 5292) to A.D. 770 ± 60 years (UGA 5297). Eleven smaller sites in the immediate area produce Raccoon Notched and triangular points; three others are related through the presence of portions of the Raccoon Notched Assemblage. Sites containing Raccoon Notched Assemblage materials are: 36 ER 19, 22, 24, 30, 33, 36, 182, 185, 186, 187, 195, 198, 203, and 207 (Figs. 1 and 30).

The 1/10 sq ha occupation on Melnick property was recorded by Neal Clark and the author in 1952. At that time the western half of 36 ER 31 was owned by Alden May and was in second-growth timber. In 1955 several test squares were excavated into the black silty soil on the May property by members of Erie Chapter No. 6 of the Society for Pennsylvania Archaeology. Recovered were Raccoon Side and Corner Notched points along with Levanna triangles. Corded, grit-tempered body sherds and several fragmentary rim sherds, apparently of Jack's Reef corded types, were found in a midden that had been partly disturbed by floodwaters from French Creek.

The Alden May property was eventually sold to Lee Port, who cleared and cultivated the western portion of the site in the 1970s. As the plow intersected village pits, a sizeable sample of pottery was recovered by Arnold Bailey of Meadville, Pennsylvania (Fig. 26f–k).

In 1983, Gannon University and CMNH initiated a joint, three-year research program in the valley of the South Branch of French Creek, utilizing the expertise of CMNH and students in a field school program, to seek answers to research problems in northwestern Pennsylvania. Efforts concentrated on the Melnick property and on land to the east, owned by

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similar to the Hopewell pottery of the Central Illinois Valley, with dentate stamping in a herringbone pattern; e. Large tip of a blade made of Coshocton, Ohio, Upper Mercer flint; f. Spurred end scraper, Coshocton, Ohio, Upper Mercer flint; g. Steuben point, Onondaga chert; h. Possible Snyders point base, Flint Ridge, Ohio, Vanport flint.

Richard Kingen. This cooperative effort resulted in the excavation of over 1,200 sq m at this important location. In addition to these excavations, related survey work recorded 19 adjacent sites, some of which were subjected to testing and/or sufficient fieldwork to document the prehistoric affiliations.

The Melnick #1 site produced nearly 7,000 diagnostic items, including 21 Raccoon Notched and 81 triangular points. A sample of representative point and tool types is shown in Fig. 25. Other stone items and ceramics are illustrated in Fig. 26: celt (a) and pendants (b, c) are similar to specimens retrieved from the Outdoor Theater site in Beaver County (36 BV 24). Study of the lithic sources indicates that of the total 4,124 items from Melnick, only 2% were manufactured from imported (Ohio) materials.

The inhabitants of the Melnick sites utilized both Raccoon Notched and triangular points but had little contact with Ohio Middle Woodland influences. Analysis of the ceramics indicates some interaction with the Regional Center at Irvine. Rim sherds of Jack's Reef Corded, Corded Collar, and Kipp Island Crisscross occur at both centers (Fig. 28b–f, Fig. 26f, g, i, j). Fig. 26h, k illustrate the internal rocker-stamping and coil or section breaks.

House patterns did not survive the deep cultivation at Melnick; however, four deep features produced radiocarbon dates. No Raccoon Notched materials were recovered from dated features; nonetheless, with a ratio of four triangular points to each Raccoon Notched form, this was not unexpected. One Levanna point from Feature 5 dated A.D. 525 ± 65 years (UGA 5292). Feature 21 contained seven Levanna points, three drills, a scraper, and fragments of Jack's Reef pottery and dated A.D. 635 ± 60 years (UGA 5427). Feature 12, dated A.D. 690 ± 60 years (UGA 5297), contained a Levanna point, Jack's Reef pottery, and calcined bone. Feature 10 contained a potter's tool, calcined bone, and butternuts (*Juglans cinerea*) and dated A.D. 770 ± 50 years (UGA 5296). Melnick #1 dates suggest that this site postdates the Middle Woodland period of influence in the French Creek Valley and that the Hopewellian dominance there terminated around A.D. 500.

The recorded Wise Mound location is about 1 km from the Regional Center Melnick sites but was destroyed by unknown excavators prior to the Gannon/CMNH study. An undisturbed hearth that had been protected by a large stump yielded a date of A.D. 160 ± 10 years (UGA 5293) and contained Flint Ridge and Onondaga flakes, some red ochre smears, and no diagnostic material. Other nearby mound recordings include Indian Head (36 ER 28) near Lebouf Creek and Mystic (C-36 ER 220) on French Creek. Sites on the Dollar farm on Stone Quarry Road (C-36 ER 195 and C-36 ER 196) produce Flint Ridge points, cache blades, gorgets, and flake knives, as evidenced by collections held by Frank Swartz of Erie. Similar materials are reported from the Lewis Farm (36 ER 33) and the now destroyed Lebouf Beach site, 36 ER 16.

Another nearby mound and village may be more closely related to the Regional Center at the French Creek Flats and perhaps participated in the Hopewell Interaction Sphere described for the Ohio area by Seeman (1979:240–248). The Danner Mound (36 CW 4) was excavated by the author and Neal Clark in 1959. Located on Oil Creek, a tributary of the Allegheny River located 15 km southeast of the French Creek Flats, this mound contained two copper crescent gorgets, copper beads, chalcedony flake knives, a large leaf-shaped blade of Coshocton flint (18 cm in length), a cache blade, a two-hole gorget, a Snyders point, and other items (Clark et al., 1960: 37–45).

Edinburg and West Pittsburgh Terraces

A cluster of Middle Woodland sites and several mounds along the Mahoning River within the Beaver drainage were of early interest to archaeologists. Several articles about the small, earthen burial mounds were published by Taylor (1878:306) and Miller (1878:168) in the *Annual Report of the Board of Regents of the Smithsonian Institution* and reported by Mayer-Oakes (1955:81). Mayer-Oakes recognized the presence of grit-tempered Mahoning ware pottery and the distinctive Raccoon Notched point type at these sites.

There are four Lawrence County sites that have produced the Raccoon Notched points in quantity: West Pittsburgh (36 LR 1) and Morrow (36 LR 5), located on the Beaver River below the town of West Pittsburgh, and the Howard Chambers (36 LR 3) and Bolinger (36 LR 21) sites on extensive terraces adjacent to the Mahoning River near Edinburg, Pennsylvania (Mayer-Oakes, 1955:81–84).

During the 1960s a series of features were exposed by deep cultivation at the Howard Chambers site. These features, excavated by Richard Gartley, contained a sizeable sample of Mahoning Cordmarked pottery in association with Raccoon Notched and triangular points (Johnson, 1976:62; John Zakucia, personal communication, 1987). Neal Clark's 1959 surface collection from this location includes Raccoon Notched, triangular points, bladelets of chalcedony, and several hematite celts.

A site reported by John Zakucia in 1986, the Ashton Cemetery site (C-36 LR 103) on the Mahoning River immediately northwest of Edinburg, also produced a sizeable collection of Raccoon Notched points. Taken altogether, the sites at Edinburg and West Pittsburgh appear to represent a settlement pattern of village relocation similar to that at Zawatski. The sites producing Raccoon Notched Point Assemblage materials are within 12 km of one another.

Earlier Middle Woodland Hopewellian material has been reported for the area by Mayer-Oakes at the Morrow site (36 LR 5). A stone crypt was excavated by George V. Morrow in 1880 and Mayer-Oakes believed that the recovered materials represented the remains of a small Middle Woodland mound (Mayer-Oakes, 1955:82, 84–85). A mound on the Chambers farm (36 LR 11) was excavated by John Zakucia in 1960. Associated burial artifacts included slate gorgets, Flint Ridge flake knives, stemmed points, a hematite cone, and a scraper. Mica, crude cache blades, Flint Ridge flake knives, and other items were found in the mound fill. Zakucia believed the mound shared Adena and Hopewell traits and saw similiarities to the Sugar Run and Irvine Mounds of the Allegheny Valley and others in New York (Zakucia, 1961:14).

The West Pittsburgh site is now completely devastated and it is assumed that additional sites that could have been part of the Edinburg-West Pittsburgh Regional Center have been destroyed by industrialization and extensive mining.

Raccoon Creek Terrace

The Outdoor Theater site (36 BV 24), the type station for the Raccoon Notched point, was a multicomponent site covering 20,000 sq m. It was located on an extensive terrace within a meander of Raccoon Creek, adjacent to and west of the town of Aliquippa in Beaver County, Pennsylvania (Figs. 1 and 30). The site was partially destroyed during the 1940s by the construction of a drive-in theater and was further damaged in 1958 with the construction of the Hopewell Township Water Pollution Control Plant. The small remaining section suffered additional damage by activities of Aliquippa Auto Recycling, Inc. (Emil Alam, personal communication, 1986). Because of these disturbances, no radiocarbon dates are available.

The Outdoor Theater site has produced the greatest concentration of Raccoon Corner Notched Assemblage materials of all the studied sites. Fourteen additional sites along Raccoon Creek and 33 locations within Beaver County also produce the distinctive tools (see Figs. 1, #30 and Appendix II). Located along Raccoon Creek and within 8 km of the Outdoor Theater site are the following sites: 36 BV 20, 23, 37, 39, 50, 59, 111, 118, 160, and 180. Alam describes the Outdoor Theater site as having concentrated occupation zones in restricted sections of the terrace (Emil Alam, personal communication, 1986).

The Raccoon Notched point type station was occupied throughout the Middle Woodland period, evidenced by the presence of Mahoning Plain pottery, cache blades, flake knives, and numerous Middle Woodland points made of Flint Ridge and Coshocton, Ohio, lithics. Points donated to CMNH by Alam include Chesser, Manker, Kiski, Murphys, Garvers, and Bennington types. The site produces all of the attributes of the hypothesized assemblage. Representative stone tools are illustrated in Fig. 23 while ceramic and stone categories are shown on Fig. 24. Pendants (Fig. 24a–c) are identical to those illustrated for the Kipp Island phase by Ritchie (1965:249).

A study of 53 Raccoon Notched points and tools from the Outdoor Theater site yielded the following breakdown of artifacts in percentages of flint types: 38% Upper Mercer flint, Coshocton County, Ohio; 38% Onondaga chert from glacial till; 21% Vanport, Flint Ridge, Ohio; 2% Plum Run, Alliance, Ohio; and 1% unidentified. The 61% total for Ohio raw materials is in marked contrast to the 2% and 2.3% totals for Ohio materials from the Melnick and Irvine sites to the north.

MIDDLE WOODLAND PHASES IN WESTERN NEW YORK AND NORTHWESTERN PENNSYLVANIA

In northwestern Pennsylvania and western New York, a cultural sequence can be projected from circa 100 B.C. to A.D. 900. Based on artifacts and settlement patterns, the region was occupied by local Middle Woodland people who participated in a cultural continuum from earlier Woodland times

(Lantz, 1982:38; Lantz et al., 1982:47). By A.D. 300, artifacts and raw materials, including some diagnostics of the Hopewell Interaction Sphere (Seeman, 1979) and possibly even Hopewell people, were moving through the Allegheny Corridor (Lantz et al., 1982; Lantz, 1984). This corridor was a migration route utilized by Paleo Indians and subsequent populations. The route is substantiated by the numbers of major Middle Woodland sites that are located along the Allegheny River from the present town of Irvine, Pennsylvania, upriver to Olean in Cattaraugus County, New York. Evidence of the movement of cultural material is also evident in the Conewango Creek drainages (Ritchie, 1965:215).

The Williams site (36 WA 1), a village and previously disturbed mound site located in Pennsylvania on Conewango Creek near the New York state line, was excavated by Alfred Guthe in 1950 (Guthe, 1951). An early date of 845 B.C. ± 300 years was obtained; however, Ritchie (1965:215) believed the date to be too early for Hopewell. More recent material from the village site in the Williams collection indicates that flake knives and Middle Woodland chalcedony points were present. During a recent disturbance of the mound, indications that the mound had been constructed over an earlier occupation zone were observed. This could have produced the early date. Johnson et al. (1979:69) confirm the earlier occupation zone at the Williams mound. The Walter Tennis collection from the Conewango Creek valley at Kiantone and Poland Center in New York also contains chalcedony flake knives and Manker and Chesser points. The Poland Center Mound in western New York, the largest recorded mound in the upper Conewango valley, also was associated with a Middle Woodland village (C-30 CH 79).

That the movement of culture was infringing on an already existing Middle Woodland base is strongly suggested by radiocarbon dates obtained from Mound Three at Irvine Flats (36 WA 29) and from dates obtained at the Rieder site (36 WA 103). While the artifacts from these two locations are not comparable, the date ranges do overlap. Rieder, with Vinette-like pottery and crude stemmed points of local Onondaga chert, yielded dates of A.D. 390 ± 80 years (GAK 5355) and A.D. 500 ± 80 (GAK 5352). In comparison, Irvine Mound Three dated A.D. 325 ± 110 (UGA 1642) for a feature containing Ohio chalcedony flake knives, sheet mica, red ochre, flakes of both chalcedony and local chert, and hard plain-collared ware (Fig. 32c–g).

While Ohio chalcedony dominates the earlier Hopewellian manifestations, by A.D. 500, all cultural ties with Ohio Hopewell seem to terminate with a possible merging of the Ohio Hopewell and local Middle Woodland cultural groups. Such a merger was described by Ritchie for the Squawkie Hill phase in New York (Ritchie, 1965:214, 215). Lithics from the Melnick site (36 ER 29), were almost exclusively of local Onondaga chert. Accordingly, the Raccoon Notched points and triangular points from the Irvine Flats Regional Center were of local Onondaga cherts, again suggesting a rapid decline of Hopewell and Ohio contacts and a subsequent shift to the total Raccoon Notched Point Assemblage after circa A.D. 500.

The Squawkie Hill Phase

Ritchie has established a progression within the Middle Woodland that addresses cultural change through time in New York (Ritchie, 1965: Fig. 1; 201–214). In central New York, Ritchie divides Middle Woodland into the Early, Middle, and Late Point Peninsula traditions while Hopewell is placed between the Early and Middle traditions of Point Peninsula. Ritchie's phases within the traditions are relevant to the research results presented here.

Ritchie's Squawkie Hill phase, based on a single date of A.D. 160 ± 100 years (Y 1276) (Ritchie, 1965:216) and within the Hopewell tradition, was established from trade (Interaction Sphere) artifacts from a mound group on Squawkie Hill adjacent to the Genessee River in western New York. Important to the understanding of Middle Woodland occupations is Ritchie's listing of the Poland Center, Killbuck, and Vandalia Mounds in New York, and Cornplanter, Sugar Run, and Irvine mounds in northwestern Pennsylvania as Squawkie Hill phase Hopewell (Ritchie, 1965:215). Ritchie stated: "In the early centuries of our era, Hopewellian traits were diffused or carried northward via the Ohio and Allegheny River into western and central New York" (Ritchie, 1965:228). Ritchie felt that the Ohio Hopewell cultural influence commenced during the latter part of Early Point Peninsula. However, after circa A.D. 500, he saw relationships between the Intrusive Mound Culture of Ohio and the Kipp Island phase of Late Point Peninsula.

Mayer-Oakes noted that Hopewellian influence was apparent in the Allegheny Valley and that the most important centers of occupation were located above Brokenstraw Creek in Warren County, Pennsylvania (Mayer-Oakes, 1955:216). The early movement of Hopewellian traits is well documented by the quantity of cultural material present at Middle Woodland Regional Centers along the Allegheny in western Pennsylvania and southwestern New York, especially at Irvine, Sugar Run, and Killbuck. Ritchie (1965:214, 215) recognized these sites as "centers of expression or development." Collectively, they evidence many Hopewellian attributes, including some defined by Seeman as the most diagnostic of the Interaction Sphere (Seeman, 1979:304, 313). Chesser Notched, Manker, and Snyders points, flake knives of Ohio flints; gorgets, platform pipes, cache blades, ear spools, copper crescent gorgets, and bear canines have been recorded in the region. Raw materials include silver, copper, galena, obsidian, mica, ochre, and steatite. Numerous burial mounds were also associated with the centers (Fig. 34).

Burial mounds of the type found at the Hopewellian-influenced Kipp Island phase 2 site in central New York (Ritchie and Funk, 1973:155) are almost unknown for southwestern New York and northwestern Pennsylvania. This may result partly from indiscriminate excavations and subsequent lack of publication. Mounds One and Three at Irvine do appear to be early and related to Hopewellian influence. Among items recorded for Mound One are sheet silver, a gorget, flake knives of chalcedony, a plain-collared rim sherd similar to the ware excavated by the author (Fig. 32c), as well as Manker and Chesser points of Ohio chalcedony. Mound Three contained an adze, a curved-base pottery platform pipe, a celt, and several Onondaga chert side-notched points similar in form to the Chesser Notched type (Carpenter, 1956:90–93; Plates 8–12, 19). Other Hopewell connections at Irvine include a feature at 36 WA 97 (Fig. 32a, b) and a feature at the Harrington farm site, 36 WA 87, across the river (Fig. 33a–h). The Hopewellian influence at the Irvine Regional Center is within the definition of Ritchie's Squawkie Hill phase (Ritchie, 1965:213–215). The differences in the content of the Irvine mounds suggests that mound construction there was continuous from the Middle Woodland Hopewell through the A.D. 500 to A.D. 950 suggested dates for the Raccoon Notched Point Assemblage.

A similar situation exists at the Sugar Run Mounds (36 WA 2), located 14 km above Warren, Pennsylvania, on the Allegheny River (Figs. 1 and 34). Mounds Two and Three of the group contained artifacts related to the Ohio Hopewell Middle Woodland and date too early to be associated with the Raccon Notched Point Assemblage. The inventory includes cache blades, side- and corner-notched points of jasper and chert, sheet copper, chalcedony flake knives, biotite, muscovite, banded slate and sandstone gorgets, a pentagonal pendant, a ceramic elbow pipe, bear canines, celts, decorated pottery similar to Illinois Hopewell, human bone and red ochre (Carpenter, 1950:184–197).

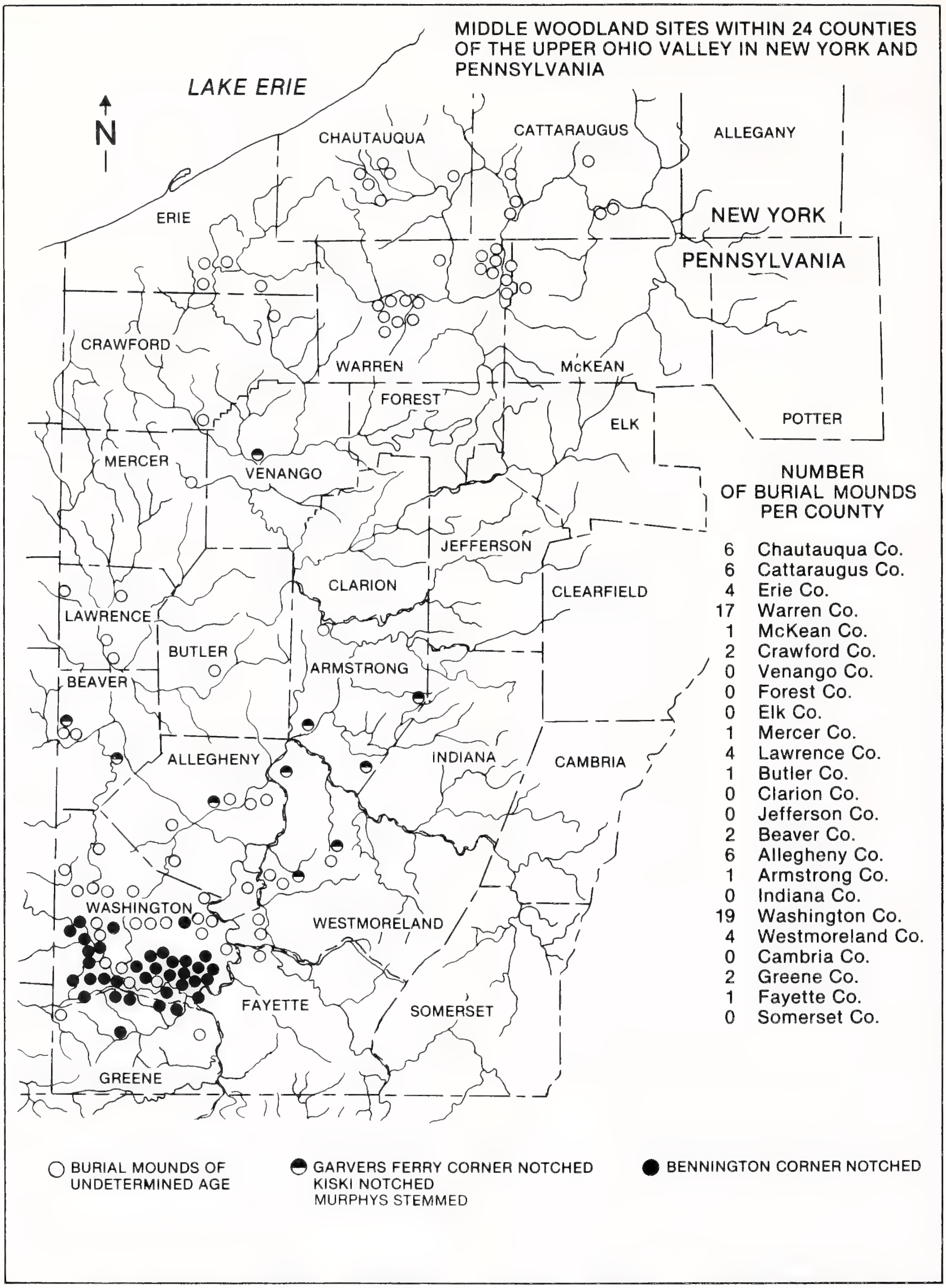
Prior to A.D. 500, Middle Woodland Hopewellian manifestations in western New York and northwestern Pennsylvania fit within Ritchie's definition of the Squawkie Hill phase.

The Allegheny River Phase, A.D. 500–950

In central New York, components of Ritchie's Kipp Island phase of Middle Point Peninsula and the Hunters Home phase of Late Point Peninsula are represented as a cultural continuum ranging from circa A.D. 500 to A.D. 900. In western New York and northwestern Pennsylvania, the distinctive Raccoon Notched Point Assemblage manifestations warrant designation as a separate phase, herein termed The Allegheny River phase. This distinct entity can be recognized in the northern Upper Ohio Valley after A.D. 500.

Extending from the upper Allegheny in Pennsylvania and New York, north toward Lake Erie (Fig. 35), the Allegheny River phase, appears to be a merger of local Middle Woodland and intrusive Hopewell cultures, culminating in the Allegheny Iroquois. It is hypothesized that the Allegheny Iroquois developed directly out of a Middle Woodland base represented in the archaeological record by the Raccoon Notched Point Assemblage. There are 42 Allegheny Iroquois sites on the upper Allegheny River in western Pennsylvania and western New York, dating from circa A.D. 940 to A.D. 1525. Cultural development through time is well supported in the ceramic assemblage where a transition from the Pre-Iroquoian pottery of New York to the Allegheny Valley Iroquois pottery occurs. The development is most comparable to the Ontario Iroquois tradition put forth by Wright (1966).

Whether it can be explained by the development of the bow and arrow or by some force that disrupted the Hopewell Interaction Sphere and the distribution of trade goods, between A.D. 500 and A.D. 600 a major transition took place in the study area. The



NUMBER OF BURIAL MOUNDS PER COUNTY

6	Chautauqua Co.
6	Cattaraugus Co.
4	Erie Co.
17	Warren Co.
1	McKean Co.
2	Crawford Co.
0	Venango Co.
0	Forest Co.
0	Elk Co.
1	Mercer Co.
4	Lawrence Co.
1	Butler Co.
0	Clarion Co.
0	Jefferson Co.
2	Beaver Co.
6	Allegheny Co.
1	Armstrong Co.
0	Indiana Co.
19	Washington Co.
4	Westmoreland Co.
0	Cambria Co.
2	Greene Co.
1	Fayette Co.
0	Somerset Co.

Fig. 34.—Distribution of sites with Bennington Corner Notched, Garvers Ferry, Kiski Notched, and Murphys Stemmed points as well as known burial mound locations.

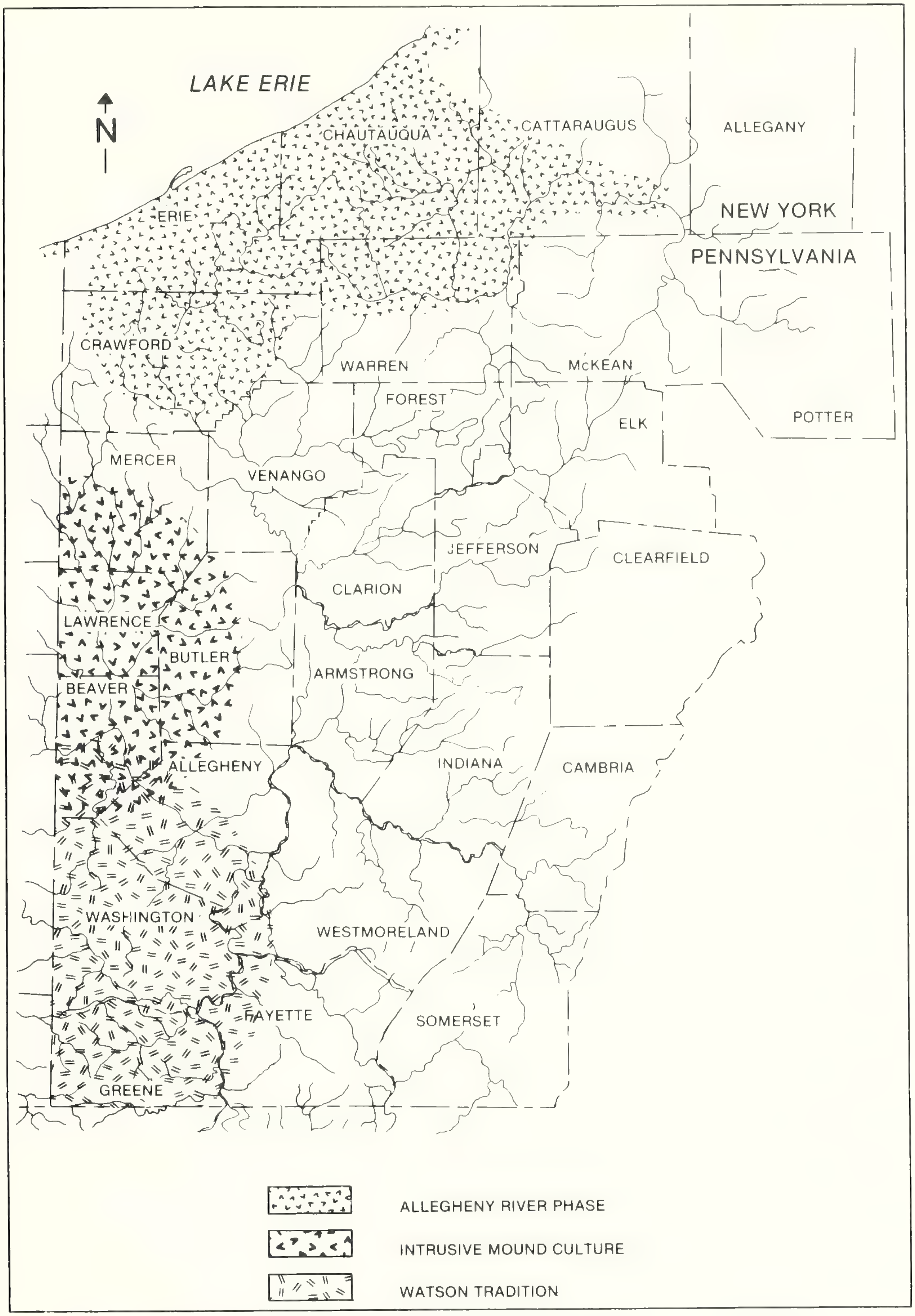


Fig. 35.—Locations of the Allegheny River phase, Intrusive Mound culture, and the Watson tradition.

heavier points such as the Chesser Notched diminished and the distinctive Flint Ridge chalcedony flake knives were fashioned almost entirely from local cherts. Raccoon Notched points are found in association with triangular points that date between circa A.D. 525 and A.D. 900. By A.D. 1000 the Raccoon forms were no longer a part of tool kits. Evidence from the Melnick site indicates that the triangular forms outnumbered the Raccoon Notched points by A.D. 600.

Village debris, although distributed over extensive areas, is thinly scattered, suggesting either widely spaced dwellings in unconsolidated villages or intermittent occupations on the same locus. The village perimeters do not appear to have been fortified which may explain the lack of consolidation. Three seasons of excavations at the Melnick site failed to locate either a palisade or a trench encircling the site, although such features are generally present in later villages associated with Allegheny Iroquois occupations. Because of deep cultivation, no house floor outlines were discerned at Melnick. All identified postmolds were mapped but no structures were evident.

While the Allegheny River phase cannot be completely defined without more extensive fieldwork, previous fieldwork and limited excavations do reveal certain artifact associations in the archaeological record. Dates for sites along the Allegheny River and along a tributary of French Creek, all located within a 100 km of one another, show few gaps within the phase (Fig. 29). Based on these dates, it is argued that the study area supported a cultural continuum through the Middle Woodland period and into Late Woodland time.

To briefly review some of the data presented above, Raccoon Notched materials were still present at the cremation burial at the Rieder site circa A.D. 830; however, the overlying strata producing Mead Island ceramics (dating circa A.D. 1020) contained only triangular points. Triangles continued in constant use throughout the Late Woodland Mead Island and Iroquois occupations.

The relationship of the Allegheny Iroquois to the Mead Island Culture (circa A.D. 840 through A.D. 1200) is currently under study (Lantz et al., 1982: 59; 1988 excavations at 36 ER 8). Mead Island appears to intrude into Iroquois country from the south and southwest and possibly could have been later absorbed into Allegheny Iroquois.

Burial mounds continued at least into the early period of triangular point utilization, although on a smaller scale. Irvine Mound Two (C-36 WA 237), located on the Irvine Flats (Figs. 1 and 34), contained Middle Woodland material that is later than Hopewell and more closely related to the Raccoon Notched Assemblage. The inventory includes a triangular point, a pendant, oxidized pyrites, a strike-a-light, red and yellow ochre, and the remains of human teeth (Carpenter, 1956:92 and Plate 16). Mound Five (C-36 WA 232), located on a bluff across the Allegheny River from the main Irvine mound group, also contained triangular points, along with a broken slate pendant, an unusual serpentine celt, and fragments of human tooth enamel. Associated with the triangular points are pendants of local siltstone and occasionally of Ohio banded slates. These have been noted in surface collections from sites dating after A.D. 500. Grit-tempered, corded pottery similar to Jack's Reef corded and Kipp Island types are found in collections from the Irvine Flats (Fig. 28b–f). Stone tools consisting of celts, sinewstones, pitted stones, and anvils have also been recovered from the surface and a stone platform pipe has been recorded at Irvine. The acidity of soils in western New York and Pennsylvania precludes the recovery of bone; it must be assumed that the bone inventories would mirror those described by Ritchie (1965:230, 231).

Data from the Melnick site (36 ER 31) show similarities in ceramics and lithics between sites on the Allegheny River and those on a tributary of French Creek. However, quantities of distinctive triangular points differentiate these two areas. Referred to as Waterford triangles, these points are similar to the Levanna point but exhibit a unique notch or deep off-center concavity on the base (Lantz et al., 1982: 65). Examples of the type are illustrated in Fig. 31a, e, i, l, and m and in Fig. 25gg and hh. The Waterford triangles were numerous at Melnick between A.D. 525 and A.D. 770 and were still present circa A.D. 1350 at the Boleratz II site (36 ER 32), located 1.2 km upstream from Melnick (M. Jude Kirkpatrick, personal communication, 1987). A rim sherd from Boleratz II with oblique trailing on an incipient collar is similar to Ripley Plain ceramics from the Middleport site in Ontario and the Ripley Triangular type from the Erie site at Ripley, New York (MacNeish, 1952:112). Waterford triangles also appear as a minority type at several sites on the Irvine Flats and at 36 WA 203 on the Brokenstraw drainage (John Zavinski, personal communication, 1983).

REGIONAL INFLUENCES

Southwestern Pennsylvania, West Virginia and Southeast Ohio

In southwestern Pennsylvania, recorded Middle Woodland sites are located predominantly to the extreme west and few are known for Greene, Fayette, Somerset, and Cambria Counties. Documentation from the CMNH files shows a concentration of Middle Woodland sites in Washington County, where 113 Middle Woodland locations and 19 associated burial mounds are recorded (Figs. 30, 34 and Appendix II). The Raccoon Notched Point Assemblage is most noticeable in Washington County near Ten Mile Creek where it is found in association with Bennington Corner Notched points. Of all the counties in the study area, Washington has the greatest number of sites (41) listing Raccoon Notched points in the inventories. This could be misleading, however, because Washington County has the highest total number of recorded sites (1,052 sites compared with only 180 in adjacent Greene County). Westmoreland County is listed as having 47 Middle Woodland sites and four mounds. Somerset County to the east has no known burial mounds.

The use of Ohio flints, methods of human interment, and the material culture express a conservative relationship with several outlying traditions. Hopewell influence is implied by the continued use of exotic Ohio flints, specific point types, and mounds with stone slab vaults. Washington County is located on the southeastern fringe of the Hopewell Interaction Sphere of the Sciota tradition (Seeman, 1979:258–263). However, the elaborate mortuary customs within the Hopewell Interaction Sphere during early Middle Woodland (200 B.C. to A.D. 400) (Seeman, 1979:237) are almost unknown in southwestern Pennsylvania and the Panhandle of West Virginia. Only the Peters Creek Mound (C-36 AL 271), excavated in 1890, contained mortuary items that are possibly Hopewell. Located near Clairton on the Monongahela River in Allegheny County, Peters Creek Mound contained two copper breastplates measuring 43.0 cm by 22.5 cm and 35.5 cm by 15.0 cm respectively; three pieces of folded copper; one stone cone; four bear canines, one still attached to a drilled jaw bone and sheathed in copper; 60 disk-shaped beads; 28 large, barrel-shaped shell beads; a fully grooved axe; three celts; and red ochre, all associated with the remains of a skeleton (Schooley, 1902:1–10).

None of the early southwestern Pennsylvania burial mounds researched by Carpenter (1950) contained diagnostics of Hopewell. As a whole, raw materials and artifacts diagnostic of the Interaction Sphere as listed by Seeman (1979:304, 313) are extremely rare although Snyders points are sometimes seen in collections.

The concentration of Middle Woodland sites and mounds and the presence of Raccoon Notched points in southwestern Pennsylvania supports Mayer-Oakes's suggestion that Raccoon Notched points were associated with Middle Woodland mounds. He stated: "While there is very little evidence to associate this point type with Middle Woodland mounds, it appears on camp sites which appear to represent this period and will be so considered for the time being" (Mayer-Oakes, 1955:87).

After A.D. 500, the Middle Woodland period in southwestern Pennsylvania appears to have been most closely related to the Watson tradition (Hemmings, 1984:47); however, there are also similarities to the Buck Garden Culture (Maslowski, 1985:27), the Peters phase (Prufer and McKenzie, 1966; Seeman, 1980:13), and the Newton focus (Seeman, 1980:1–3).

The Watson Tradition

Hemmings (1984:47) describes the Watson tradition as a "distinctive cultural tradition that emerged, developed, and flourished in the Upper Ohio Valley." He further described the tradition as "a conservative and successful adaptation" that could be recognized from circa A.D. 180 until agriculture and villages of the Monongahela appear by A.D. 1000. This development into Monongahela was also suggested by Maslowski (1985:30). The Watson tradition was named after the Watson Farm site (46 HK 34) and associated burial mounds within the northern Panhandle of West Virginia (Hemmings, 1984).

While evidence that southwestern Pennsylvania was heavily influenced by the Watson tradition is not overwhelming, reported sites and a few dates show that some Watson traits did penetrate the area. The Watson village and associated mound (46 HK 34) were reported by Dragoo (1956). The site produced mostly limestone-tempered Watson Cordmarked pottery along with a smaller percentage of grit-tempered Mahoning Ware. Flint Ridge chalcedony was present in the lithic industries of both the mound and the village. Artifacts included flake knives. Chesser Notched points, and other notched varieties of points.

The predominant occupation at Watson was radiocarbon dated between A.D. 500 ± 100 years and A.D. 930 ± 55 years. The earlier date of A.D. 500 is from a hearth reported as predating the Watson Mound occupation (McMichael, 1968:62), while the A.D. 930 date is one of several obtained by a University of Pittsburgh field school at the Watson village site (Maslowski, 1985:26).

Hemmings has proposed that the Watson site was an integral unit of a cultural tradition that flourished in the Upper Ohio Valley from the first millennium A.D. This Watson tradition emerged from a Hopewellian mortuary ceremonialism and trade network, climaxing in Ohio by A.D. 200; however, it continued as a significant, but continuously diluting Hopewellian manifestation (Hemmings, 1984).

Perhaps one of the most important mounds related to the Watson tradition is the Pollocks Hill Mound (C-36 WH 1051), located above the Monongahela River in Union Township, Washington County. This mound was salvaged by George S. Fisher in the early 1930s during its almost complete destruction by numerous excavators (Cadzow, 1933: 3–5, 16). Artifacts recorded consisted of two rolled copper beads, a celt, Manker and Chesser Notched points, an untyped stemmed and side-notched point, two drilled bear canines, two bone fish hooks, and, most importantly, a Raccoon Pentagonal Corner Notched point (Cadzow, 1933:16; Fig. 8, #7). With the exception of the bear canine, copper beads, and the Raccoon Notched point, the material from this mound is similar to material from the Avella Mound (Verna Cowin, personal communication, 1988).

The Avella Mound (36 WH 415) was excavated near Avella in Washington County by the University of Pittsburgh (Applegarth and Cowin, 1982:241). This mound, investigated by Cowin from 1975 to 1978, is believed to be a late expression of the Watson tradition but no ceramics were recovered (Verna Cowin, personal communication, 1987). Radiocarbon dates of A.D. 530 ± 115 years (SI 3499), A.D. 790 ± 110 (SI 2943), and A.D. 850 ± 90 (SI 3498) were reported (Applegarth and Cowin, 1982:254). Of note is the association of a Bennington Corner Notched point with the A.D. 790 ± 110 date (SI 2943).

Another pertinent mound excavation is the McKees Rocks Mound in Allegheny County. This mound was investigated by CMNH in 1896; the mound and associated materials were subjected to reanalysis by Edward V. McMichael of Indiana University in 1956. McMichael saw relationships of some of the artifacts to New York Hopewellian materials and also to the upper Allegheny in northwestern Pennsylvania. However, he noted that he saw a closer relationship to the Watson Mound (McMichael, 1956:144).

Richard L. George of CMNH completed excavations in 1984 at a Middle Woodland site having Watson and Mahoning ceramics along with flake knives and points of Flint Ridge chalcedony. This Westmoreland County site, the Billy site (36 WM 677), is associated with the Billy Mound (36 WM 50). George reports that the Billy Mound was completely disturbed by previous excavators (personal communication, 1986).

Located within the northern Panhandle of West Virginia, the Fairchance site, excavated by Hemmings in 1984, represents an important phase within his Watson tradition. Radiocarbon dates from the mound and village place the occupation at circa A.D. 150. At Fairchance, Watson Ware predominated and the lithic assemblage bears similarities to that of the Watson site. Raccoon Notched and triangular points have not been included as diagnostics with the Watson tradition; however, they have been found in surface collections from the Watson site where triangular points are more common than the Raccoon Notched forms.

Based on the sites and dates presented above and data in the CMNH site files (See Appendix II) a proposed sphere of influence for the Watson tradition is shown in Fig. 35. The post-Hopewellian period in southwestern Pennsylvania is best represented within the Watson tradition. Furthermore, future research may prove that the Raccoon Notched points, the Bennington Corner Notched point, and triangular points should be included as diagnostics within this tradition. It is likely that the triangular point emerges at a later date in southwestern Pennsylvania than it does in northwestern Pennsylvania and western New York.

The Buck Garden Culture, the Peters Phase and the Newton Focus

There is a remote chance that the Buck Garden Culture of central West Virginia could be related to the post-Hopewellian period in southwestern Pennsylvania. The Buck Garden Culture, radiocarbon

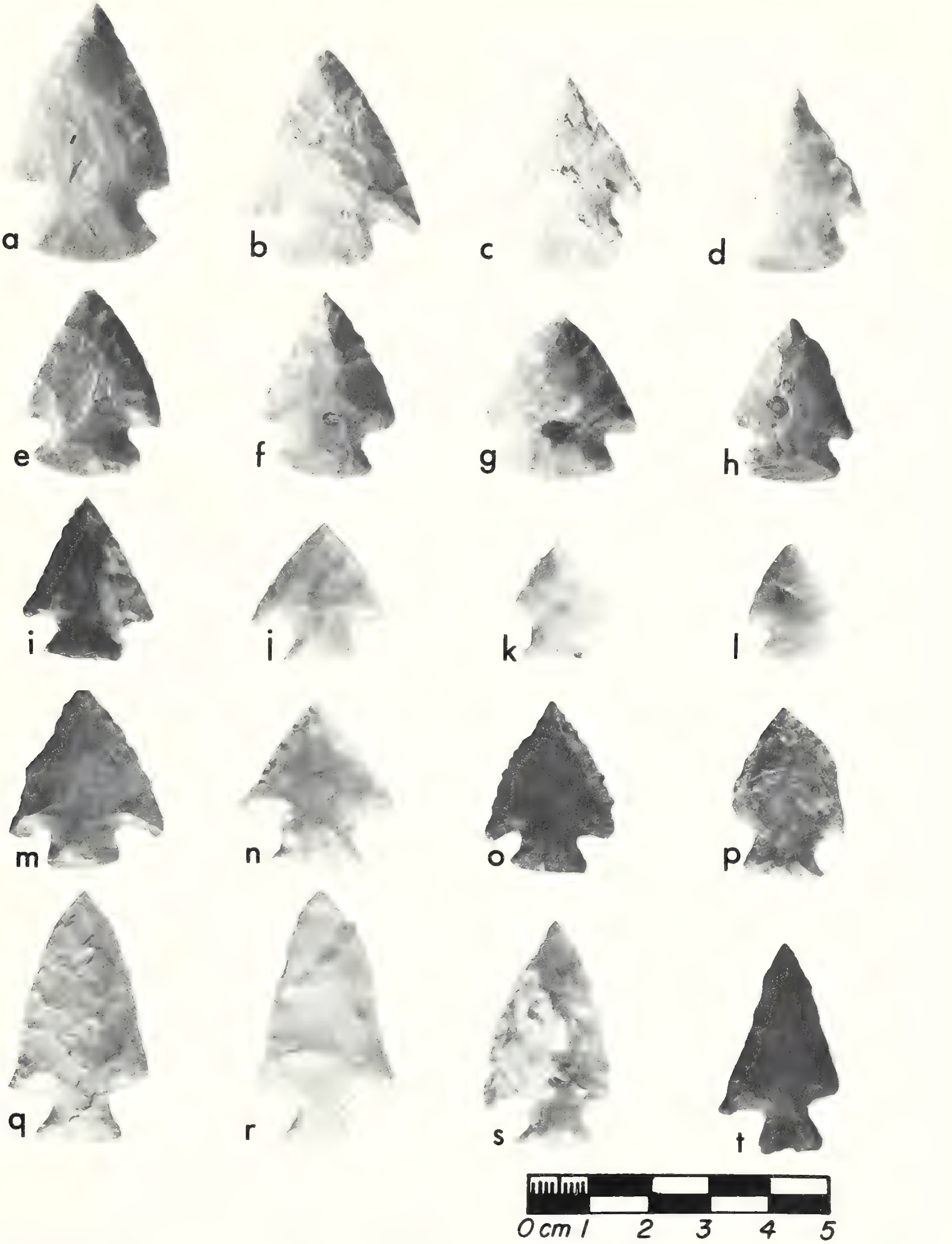


Fig. 36.—Middle Woodland points by type, material of manufacture, and provenience. Bennington Corner Notched: a. Loyalhanna, C-36 WH 1044; b. Flint Ridge, 36 WH 443; c. Unknown, 36 WH 786; d. Flint Ridge, 36 WH 443; e. Uniontown, 36 WH 662; f. Onondaga, 36 WH 824; g. Flint Ridge, C-36 WH 1045; h. Ten Mile, 36 WH 824. Kiski Notched: i. Coshocton, 36 WM 30; j. Flint Ridge, 36 BV 68; k. Flint Ridge, 36 AL 19; l. Flint Ridge, 36 WM 140. Garvers Ferry: m. Onondaga, 36 BV 24; n. Flint Ridge, unknown; o. Unknown, 36 AL 19; p. Coshocton, 36 BV 68. Murphys Stemmed: q. Chalcedony, unknown; r. Flint Ridge, 36 VE 11; s. Flint Ridge, 36 BV 68; t. Coshocton, 36 AR 29.

dated from A.D. 690 ± 110 years (RL 1191) to A.D. 1012 ± 110 years (RL 1192), has triangular points, stemmed and expanding-stemmed points including Chesser Notched, and ceramics similar to Watson Ware (Maslowski, 1985:27). Many mounds in central West Virginia are attributed to this complex (McMichael, 1968:26–29; Maslowski, 1985:23). It is important to note that the Bennington Corner Notched point (Fig. 36a–h) is comparable to a type illustrated by McMichael (1968, Fig. 28h).

A similar taxonomy is reported for the Peters phase of southeastern Ohio (Prufer and McKenzie, 1966; Seeman, 1980:13). Seeman places the Peters phase at circa A.D. 500 to A.D. 800 and recognizes a similarity between Peters Cordmarked and Watson Cordmarked pottery. The Peters phase lithics include triangular points, Chesser Notched points, and fishspears.

The Newton focus (circa A.D. 500 to A.D. 800) of southern Ohio is described by Seeman (1980:1–3) as occupations of 1.2 to 2.0 ha on elevated floodplain terraces and associated with mounds containing stone-covered interments. Diagnostics are identified as Chesser Notched points, chipped flint, ground stone celts, stone discs, thin rectangular state gorgets, large pentagonal knives, vertical cordmarked pottery with angular shoulders (Newton Cordmarked), and bone tools. Triangular points and prismatic blades are not recognized within this assemblage.

Seeman (1980:17) emphasizes that the Peters phase and the Newton focus lack precise definition, suggesting that the emphasis should be put on site similarities rather than on slight attribute differences. He suggests that, as a group, they should be referred to as the Central Ohio Valley Early Late Woodland. Geographically, this would include the general area of Pittsburgh, Pennsylvania, west to Cincinnati, Ohio. The Central Ohio Valley Early Late Woodland, as suggested by Seeman (1980:17), overlaps the Middle Woodland Watson tradition occupations (Hemmings, 1984:47).

The Bennington Corner Notched Point

Bennington Corner Notched points have a considerable presence in southwestern Pennsylvania. They are found in concentrations along branches of Ten Mile Creek in Washington and Greene counties and often near mounds. This point type (Fig. 36a–h) was first referred to as a Quail Tail by Howard Keys around 1940 (William Bennington, personal communication, 1988); Fogelman (1984) calls the form the Bennington Quail Tail. In 1981, James Herbstritt recognized these points in the collection of William H. Bennington of Washington County and suggested the name Bennington Corner Notched. The point was described as triangular and broad, exhibiting pronounced corner-notching on a thin blade which thickens toward the base (William Bennington, personal communication, 1987). A radiocarbon date of 790 ± 110 years (SI 2943) was obtained on a Bennington Corner Notched point found in association with a burial in the Avella Mound in Washington County (Applegarth and Cowin, 1982:241).

Most of the Bennington Corner Notched points examined have excurvate bases resembling the tail of a quail; however, some are almost straight. A similarity in outline is seen with Type 2B of the Raccoon Assemblage (Fig. 5); however, the Bennington Corner Notched point has a thicker base. One of the main characteristics of Raccoon Notched points is their thinness from the blade tip to the base with the sample averaging 2.2 mm at the base. The average blade thickness for the Bennington Corner Notched point as described by Boldurian is from 5 to 6 mm (Boldurian, 1985:171). Generally, these points were manufactured of local Ten Mile flint but other exotic materials were also utilized (James Herbstritt, William Bennington, personal communications, 1986).

Unlike the northwestern counties of Pennsylvania where glacially transported Onondaga cherts were available, southwestern Pennsylvania had outcrops of quality lithics in Lawrence, Washington, Greene, Fayette, and Westmoreland counties. These sources include the Zaleski Member of the Allegheny Formation (Sky Hill Flint) (Stout and Schoenlaub, 1960: 8), the Uniontown Formation of the Monongahela Group reported by Eisert (1974:32–39), the Greene and Washington Formation of the Dunkard Group (Ten Mile Flint), the Pittsburgh Formation of the Monongahela Group (Sewickley Flint), and the Brush Creek Member of the Conemaugh Group (Brush Creek Flint), all reported by Herbstritt (1981:1–9). Bennington reports that a number of the points bearing his name were manufactured from imported Flint Ridge materials while others were produced from local and semiexotic varieties of the above-named types.

Lithic sources differ widely in southwestern Pennsylvania in comparison with what has been reported for northwestern Middle Woodland. In the south, Flint Ridge chalcedony and Coshocton, Ohio, lithics do not fade from the record at the time the small, notched forms of projectile points appear. Thus it is important to identify the geographic boundaries for the Bennington or Quail Tail points.

Since this point is a recently described type, its name does not appear on older survey records. Review of photographs and drawings and personal interviews of collectors in southwestern Pennsylvania segregrated Bennington point recordings by county: 20 were recognized in Washington, five in Greene, and one in Beaver. This inventory was reviewed by Bennington as well as by Bill Ringlesbach of McDonald, Pennsylvania, and these two long-term collectors verified 39 locations that produce the type. At 12 of these sites, Raccoon Notched points and triangular points were found in association while 19 others had the Bennington forms in association with Raccoon Notched material but no triangles. Plots for the Bennington finds and associations are shown on Fig. 34 and the locations are documented in Appendix II. The Cowden #2 site in Washington County has the heaviest concentration of Raccoon Notched and Bennington Corner Notched points in association; no triangular points are reported at Cowden #2, suggesting that triangular points may date later in southwestern Pennsylvania.

Summary

In southwestern Pennsylvania, the elaborate mortuary customs of Middle Woodland are present; however, they are weakly expressed. From this Middle Woodland base, perhaps through a blending of local and intrusive traditions, a diluted Middle Woodland manifestation was retained in the area. This manifestation is most closely aligned with traits of the Watson tradition. Future research may add the Raccoon Notched, Bennington Corner Notched, and triangular points to the Watson trait list. Current evidence suggests that the replacement of notched point varieties by triangles may date later in the south.

Central Western Pennsylvania and Eastern Ohio

The only excavations reported for the central region of western Pennsylvania are the Chambers Mound (36 LR 11), excavated by John Zakucia (1961) in the 1950s; the Boarts site (36 LR 36) in 1971–1972 and reported by the University of Pittsburgh (Adovasio et al., 1974); and the Morrow site (36 LR 5) (Mayer-Oakes, 1955:83–85). Any other interpretation of this region must be gleaned from Mayer-Oakes and recordings in the CMNH site files.

The Chambers Mound had some Hopewell attributes, namely a Snyders point fragment, Chesser Notched points, bladelets of chalcedony, complete two-hole gorgets, a hematite cone, Mahoning Ware ceramics in the mound fill, and other diverse cultural items (Zakucia, 1961). The Boarts site is recorded as a multicomponent lithic workshop. Middle Woodland material reported from the Boarts excavation and from private collections include Chesser Notched and Snyders-like points (Adovasio et al., 1974:48). The Morrow site contained large gorgets, a copper sheathed mica crescent, and a large copper bead. The Chambers Mound, Boarts, and Morrow site materials attest to some degree to ceremonialism of Hopewell influence in the Mahoning drainage at an early time period.

In adjacent eastern Ohio, Mayer-Oakes (1955:82, 83) reported on a mound in Trumbull County (33 TR 5), north of the Mahoning drainage. This mound was partially excavated by Zakucia, Platt, and Wakefield in 1951 and contained flake knives of chalcedony, a Snyders-like point base, slate gorgets, copper hemispheres, grit-tempered pottery, cache blades, and other items. The North Benton Mound, on the upper Mahoning drainage in Ohio, contained more diagnostic Hopewell material. This large mound was excavated in the 1930s and contained a limestone platform pipe, chalcedony flake knives, ear spools, copper hemispheres, a breastplate, a panpipe, silver, galena, mica, and other Hopewellian artifacts (Magrath, 1945:42–45; Mayer-Oakes, 1955: 82).

The central counties of western Pennsylvania are within the fringe of the Hopewell Interaction Sphere as defined by Seeman (1979) and, earlier, by Struever and Houart (1972:48–52). This sphere of influence declined by A.D. 500. During the Hopewell climax, artifacts and cultural ideas were moving east and north along the valleys of the Ohio and Mahoning Rivers, as well as through the Allegheny Valley's Regional Centers as exemplified by the Irvine Flats, Sugar Run and Killbuck sites (Carpenter, 1950; 1956). Seeman suggests a connection with the New York Point Peninsula (Seeman, 1980:18). This connection was also noted by Ritchie when discussing the diffusion and momentum of Hopewellian traits into western New York by way of the Ohio and Allegheny Rivers (Ritchie, 1965:228).

As noted earlier in this report, all cultural ties with Hopewell terminate in the upper Allegheny by

A.D. 500. This is not the case in the west central counties. Here the connections continued into later Middle Woodland time—during the period when the Raccoon Notched Point Assemblage was utilized. In Lawrence and Beaver counties, adjacent to the Ohio line, Raccoon Notched point sites are clustered on the Mahoning and Raccoon Creek drainages (Fig. 1). The Raccoon Assemblage tools were manufactured primarily from Vanport chalcedony from Flint Ridge and Upper Mercer flints from Coshocton County, Ohio.

At the Morrow (36 LR 5) and Chambers (36 LR 1) sites in Lawrence County and at the Outdoor Theater site (36 BV 24) in Beaver County, numerous Chesser Notched points, triangular points, and Raccoon Notched points have been collected from the surface. Mayer-Oakes (1955:81) reported a steatite platform pipe of the Intrusive Mound type from a site near Edinburg (36 LR 3). More recently, Richard Gartly reported Raccoon Notched points in association with triangular points and Mahoning Ware ceramics at 36 LR 3 (Johnson et al., 1979:62).

The Intrusive Mound Culture

Based on the data presented above, the Middle Woodland cultural material of west central Pennsylvania seems most associated with the Intrusive Mound Culture of southern Ohio, as described by Morgan (1952:83–98) and Seeman (1980:11–13). The Intrusive Mound Culture may be represented in Pennsylvania from Lawrence County south through Beaver County, based on the distribution of Raccoon Notched points, triangular points, keeled-base platform pipes, pendants, and Mahoning ceramics. Johnson et al. (1979:83) report that ceramics from the Edinburg site (36 LR 3) are similar to those of the Intrusive Mound Culture of Ohio. The Intrusive Mound Culture, or a similar phenomenon, rapidly dissipated to the south in Washington and Greene counties and to the east in Westmoreland and Fayette counties. There is no evidence of the Intrusive Mound Culture in Cambria and Somerset counties. However, because of cultural overlap and diffusion, traits of the Intrusive Mound Culture occasionally coexisted with the Watson tradition.

Mayer-Oakes recognized that Middle Woodland populations were selecting fine-grained, exotic flints for the production of Raccoon Notched points in the area now comprising Lawrence and Beaver counties and included the lithic preferences in the original type description (Mayer-Oakes, 1955–1987). The same observation was noted by Alam (1972) and Zakucia (personal communication, 1986). This preference for exotic lithics is significant, as it is in sharp contrast with what has already been documented for the upper Allegheny drainage. Ohio flints accounted for only 2.3% of the Raccoon Notched Assemblage at Irvine and only 2% at Melnick.

In view of the statements by Mayer-Oakes, Zakucia, and Alam, an analysis of 53 Raccoon Notched points from the Outdoor Theater site, the type station (36 BV 24) was conducted. The results show that Coshocton County, Ohio, Upper Mercer flint accounted for 38% of the sample; glacial outwash Onondaga cherts were also 38% of the total. The remaining distribution showed that 20% was of Flint Ridge chalcedony and 2% was of Plum Run flint from Alliance, Ohio, while the remaining 2% was from unknown sources. The utilization of Ohio lithic sources may have resulted from availability. The northern sites in this study are situated 225 km away from the Flint Ridge and Coshocton quarries compared with the 120 km between the Outdoor Theater site and the exotic lithic sources.

Garvers Ferry Corner Notched, Kiski Notched, and Murphys Stemmed Points

In 1982, three Middle Woodland points, Garvers Ferry Corner Notched (Fig. 36m–p), Kiski Notched (Fig. 36i–l), and Murphys Stemmed (Fig. 36q–t) were described and assigned names by Richard L. George of CMNH (George, 1982:205–209). George lists seven sites with various combinations of these points and currently a total of ten locations are known to have produced these points (Appendix II and Fig. 34).

Based on the stratigraphic position of the Garvers Ferry Corner Notched point at the Blawnox site (36 AL 19), George places the type as Middle Woodland or early Late Woodland. Likewise, he sets the time for the Kiski Notched point at late Middle Woodland. The Murphys Stemmed point was documented on sites that had Middle Woodland affinities (George, 1982:205–209).

The geographic range of this point group was recently expanded westward to drainages in Beaver County. Archaeological material from the Outdoor Theater site (36 BV 24), the Raccoon Notched type station, was examined by George and the author. George verified the presence of his newly defined Middle Woodland types in Emil Alam's collection. Several Bennington Corner Notched points were also in the Outdoor Theater site inventory. It should be noted here that the Bennington Corner Notched and the Garvers Ferry Corner Notched points are technologically quite similar (James Herbstritt, personal communication, 1986; Boldurian, 1985), as is the Bennington Quail Tail (Fogelman, 1984). The Outdoor Theater site was occupied throughout the complete range of the Middle Woodland period; therefore, the association of Raccoon Notched, Garvers Ferry Corner Notched, Kiski Notched, Murphys Stemmed, Bennington Corner Notched, and triangular points could be expected here.

Various point types are also represented at the Coble Farm site (36 BV 68) recorded in 1975. This site dates within Middle Woodland, but probably prior to A.D. 500. Coble lacks Raccoon Notched and triangular points but does include Garvers Ferry, Kiski Notched, Murphys Stemmed, reworked Snyders, Chesser Notched, and Manker Stemmed points, along with chalcedony flake knives, cache blades, and rectangular, two-hole gorgets. While most of the lithics at Coble were produced from Sky Hill (Zaleski) and Onondaga varieties, 40% of the lithics were from Ohio sources. There were also minor representations of southwestern Pennsylvania's Loyalhanna and Uniontown flints. The presence of Uniontown material suggests a northward movement of the Bennington Corner Notched point. Ceramics have never been recovered at Coble Farm, thus this location may have served as a hunting station operating within the Hopewellian Interaction Sphere (Seeman, 1979:258–263). The collections from the Coble Farm site hint that Garvers Ferry Corner Notched, Kiski Notched, and Murphys Stemmed points predate A.D. 500 at that location. However, the inventory from the Outdoor Theater site indicates that these forms continued into later Middle Woodland.

The new point types, Garvers Ferry, Kiski Notched, and Murphys Stemmed, were in use during the span of the Hopewell Interaction Sphere and continued into the period when Raccoon Notched tools were utilized. Presently George's types are represented in central western Pennsylvania; however, this distribution may widen as additional studies are made of collections.

Summary

West central Pennsylvania from circa A.D. 500 to A.D. 950 appears to be most closely related to the Intrusive Mound Culture of southern Ohio, based on the presence of Raccoon Notched and triangular points, pentagonal knives, and a similar form of platform pipe. The exotic lithics reinforce the Ohio connection as does the presence of Mahoning ceramics. In contrast with the case in the north, the use of Ohio lithics does not decline with the introduction of the Raccoon Notched Point Assemblage.

CONCLUSIONS

The major concern of this report has been to establish the Racoon Notched point, first described by Mayer-Oakes, as a major type with widespread distribution in the Upper Ohio Valley in Pennsylvania and New York. Two hundred thirty-six sites were identified as having the type. The distribution of sites has been documented by Fig. 1 and listed by county in Appendix II. The research to collect this data covered a four-year period and involved the review of over 5,500 site forms housed at CMNH. Regional conservation archaeologists and field associates of the Museum contributed additional data as did the documentation of major private collections within the study area.

Five Raccoon Notched point types have been defined and described, including the range of variation within each type. Also identified were related tools, including four knife forms, four drill types, scrapers, and strike-a-lights. It was recognized that the point and tool types as a group were found on major Raccoon Notched point sites throughout the Upper Ohio Valley; therefore, the term assemblage was applied to the artifact group. Documentation of the Raccoon Notched Point Assemblage as an entity came from three major locations: Buckaloons (36 WA 99), Melnick (36 ER 31), and the Outdoor Theater site (36 BV 24). The assemblage and associated ceramics from these three locations are illustrated in Figs. 23–28.

The date range for the Raccoon Notched Point Assemblage in northwestern Pennsylvania and western New York commences after A.D. 500 and terminates at A.D. 950. Although few dates were available, the interval was established from dated components of earlier and later cultures bracketing the Raccoon Notched materials. Further substantiation of the date range was obtained from radiocarbon determinations on similar manifestations in New York and Ohio.

After compiling the site information and plotting the distribution of Middle Woodland sites, associated Middle Woodland tools, and burial mound locations, it became apparent that certain areas were focal points for Middle Woodland activities. As a result, seven Regional Centers were designated: Zawatski, Hotchkiss, Sugar Run, Irvine, French Creek, Edinburg, and Raccoon Creek. These centers and their ancillary sites are shown in Fig. 1.

Following the distributional studies and the identification of tool types and lithic sources for manufacturing the tools, regional variations were observed. Ritchie's Squawkie Hill phase within the Hopewell tradition in central and western New York shows a mingling of Hopewell with local complexes circa A.D. 160 that dissipated by A.D. 500 to blend into the Kipp Island phase (Ritchie, 1965:213–215; 232–252). Along the Allegheny River in western Pennsylvania and western New York a culture developed from a similar cultural base (Squawkie Hill phase). It eventually replaced the Kipp Island lithics with the Raccoon Notched Point Assemblage.

In the Raccoon Assemblage, side-notched points are most prevalent, accounting for 66% of the total. Corner-notched points, similar to Jack's Reef Corner Notched, make up only 34% of the total. There are obvious differences in point sizes; Raccoon Notched points are smaller than the Jack's Reef points of the Kipp Island phase.

Another point identified and illustrated is the Waterford Triangle (Fig. 31a, e, i, l, m), a distinctive point found mostly on the French Creek drainage. Waterford Triangles are dated at the Melnick site (36 ER 31) from A.D. 525 to A.D. 770. They were retained as late as circa A.D. 1350, based on their presence at the Boleratz II site (36 ER 32). It was also noted that the later Ontario Iroquois ceramics found on Allegheny Iroquois sites to the east have not been recovered in the French Creek valley. It is entirely possible that additional research will define an additional phase or phases and refine the Allegheny River phase proposed in this publication.

The Allegheny River phase is recognized in the upper Allegheny drainages in Pennsylvania and New York (Fig. 35). Considered to be a merger of local Middle Woodland and Intrusive Hopewell, a cultural continuum to the Allegheny Iroquois is proposed and the case is made through a series of radiocarbon dates. The dates for the Allegheny River phase, A.D. 500 to A.D. 950, coincide with those of the Raccoon Notched Point Assemblage.

In southwestern Pennsylvania, the period when Middle Woodland Raccoon Notched points were utilized overlaps the Watson tradition and evidence shows strong ties to that tradition. Traits described are Watson Cordmarked and Mahoning Ware pottery, corner-notched points (some of which are comparable to the Chesser Notched type), flake knives, Flint Ridge lithics, and stone-lined burials in mounds (Maslowski, 1985:26; Dragoo, 1956:73). Support of the southwestern Pennsylvania Middle Woodland relationship with Watson comes from the association of a Raccoon Notched pentagonal with a Chesser Notched type at Pollocks Hill Mound (Cadzow, 1933:16). It is suggested that Bennington Corner Notched and triangular points became part of the Watson tradition sometime after its development from a Hopewellian-like base, the Fairchance phase, as described by Hemmings (1984:47). A Bennington Corner Notched point was found in association with a burial at the Avella Mound in Washington County, Pennsylvania, and dated at A.D. 790 ± 110 years (Applegarth and Cowin, 1982:254). Although no ceramics were found at the Avella Mound, the excavator believes the structure was associated with the Watson tradition (Verna Cowin, personal communication, 1987).

The Buck Garden Culture of central West Virginia evidences an association of triangular points with expanding-stemmed points including Chesser Notched. Ceramics are similar to Watson Ware (Maslowski, 1985:27) and it is possible that triangular points may be part of the Watson tradition. Another connection with the Buck Garden Culture can be noted in the similarities of the Bennington Corner Notched form to a point illustrated by McMichael (1968:Fig. 28h). Similar forms are also seen in the Peters phase of southeastern Ohio where dates range from A.D. 500 to A.D. 800 (Prufer and McKenzie, 1966:247–248; Seeman, 1980:13). Peters phase and Newton focus diagnostics include Chesser Notched points and pentagonal knives.

In west central Pennsylvania, the Raccoon Notched point and associated materials seem most closely aligned with the Intrusive Mound Culture of Ohio or a similar culture as yet undefined. Mahoning ceramics are similar to the Intrusive Mound types (Johnson et al., 1979:83), and Raccoon Notched and triangular points of exotic flints, pendants, and the keeled-base platform pipe are diagnostic of the Intrusive Mound Culture.

Before A.D. 500, west central Pennsylvania was within the Hopewell Interaction Sphere as defined by Seeman (1979), and evidenced by artifacts from the Chambers Mound (36 LR 11), the Morrow site

(36 LR 5), and the Boarts site (36 LR 36). The area appears to be a pathway of Hopewellian influence into the upper Allegheny.

Since systematic research-oriented archaeological excavations of Middle Woodland village sites are lacking, any synthesis of occupations between A.D. 500 and A.D. 950 must rely on available data. Carpenter's survey in the 1940s focused on the more obvious prehistoric burial mounds of the Upper Ohio Valley. Excavations resulting from Carpenter's survey concentrated in areas above the then-proposed Kinzua Dam. The majority of the mounds excavated and reported are now destroyed and many of the unexcavated, associated Middle Woodland village sites were either destroyed by gravel mining operations or inundated after the completion of the Kinzua Dam and the filling of the Allegheny Reservoir. Few known major Middle Woodland village sites remain in western Pennsylvania because they tend to be located on or near large floodplains and glacial outwash terraces already bisected by railroads or highways. Many choice site locations have been altered by flood control projects, housing developments, surface mineral exploitation, and industrialization.

The loss of the villages is further complicated by a lack of records on the full range of upland sites. These locations tend to be small hamlets or special function stations. While these resources may be extant, many are in remote wooded and uncultivated locations.

Utilizing available data, this exercise has shown that Hopewell interaction with Middle Woodland groups in western Pennsylvania and western New York diminished during the period when the Raccoon Notched Point Assemblage was being utilized. Whereas Middle Woodland Regional Centers may once have participated in major trade networks, after burial ceremonialism declined, they became more localized and relied on their advantageous locations and their satellite sites for the raw materials and the subsistence resources needed to support resident and itinerent Middle Woodland populations. Only in the west central area of Pennsylvania did the ties to Ohio remain somewhat intact, and there geography and the proximity of lithic resources may have played a more important role than did actual cultural contact. In the west central zone, the exotic lithic sources were close enough to have been tapped as part of a routine procurement strategy.

In northwestern Pennsylvania and western New York, one does not have to look for major, outside, cultural influences to find roots for what follows in the Late Woodland period. These roots were fully established in a cultural continuum from at least Middle Woodland time.

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APPENDIX I

Measurements in centimeters; AL = Artifact Listing; L = Length; W = Width; BW = Base Width; SW = Shoulder Width; MT = Maximum Thickness; BT = Base Thickness; DN = Depth of Notch; SL = Stem Length; BL = Blade Length; Wt = Weight (in grams); LM = Lithic Material; SN = Site Number; C = Collector; Inc = Incomplete. Artifact Collector abbreviated as follows: A = Alam, B = Buker, S = Stuart, Z = Zavinski. Lithic material utilized (flint type and source) abbreviated as follows: O = Onondaga (Glacial)—Pennsylvania, New York, Ohio, Ontario; C = Upper Mercer—Coshocton Co., Ohio; D = Delaware (Onondaga)—Pennsylvania, New York, Ohio, Ontario; F = Vanport (Flint Ridge)—Licking Co., Ohio.

Raccoon Side Notched Points with Excurvate Blades

Type 1

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	3.4	2.1	2.0	2.2	0.4	0.3	0.4	0.9	2.5	Inc	O	36WA99	S
2	4.0	2.0	1.4	1.9	0.4	0.2	0.4	0.7	3.3	Inc	O	36WA102	S
3	4.0	2.1	2.0	2.0	0.3	0.3	0.4	0.9	3.1	Inc	O	36WA31	S
4	4.2	2.2	1.9	1.9	0.4	0.3	0.4	0.7	3.5	Inc	D	36WA31	S
5	4.0	2.2	1.9	2.2	0.5	0.2	0.4	0.7	3.3	Inc	C	36WA29	S
6	4.2	2.3	2.1	2.2	0.4	0.3	0.5	1.2	3.0	Inc	O	36WA98	S
7	4.3	2.2	1.9	2.1	0.5	0.3	0.4	1.0	3.3	Inc	O	36WA98	S
8	4.1	2.2	1.8	2.2	0.4	0.2	0.4	0.8	3.3	Inc	O	36WA96	S
9	3.9	2.4	1.8	2.4	0.5	0.3	0.5	0.9	3.0	Inc	O	36WA98	S
10	4.3	2.2	1.9	2.4	0.5	0.3	0.4	0.9	3.4	Inc	O	36WA29	S
11	3.4	1.9	1.4	1.9	0.5	0.3	0.4	0.9	2.5	3.3	O	36WA29	Z
12	3.2	2.0	1.8	2.0	0.3	0.2	0.5	0.9	2.3	Inc	D	36WA97	S
13	4.9	2.8	2.2	2.5	0.4	0.3	0.6	1.0	3.9	Inc	O	36WA99	Z
14	3.6	1.8	1.7	1.9	0.3	0.2	0.4	0.9	2.7	Inc	O	36WA99	Z
15	3.8	2.1	1.9	2.1	0.4	0.3	0.4	0.9	2.9	Inc	C	36WA99	Z
16	3.7	2.1	2.0	2.1	0.4	0.2	0.5	0.9	2.8	Inc	O	36WA99	S
17	3.3	1.8	1.5	1.8	0.4	0.3	0.4	0.8	2.5	Inc	O	36WA99	Z
18	3.0	1.6	1.4	1.5	0.3	0.2	0.3	0.8	2.2	Inc	O	36WA98	S
19	2.4	1.8	2.0	1.8	0.4	0.3	0.3	0.9	1.5	2.2	O	36WA98	S
20	3.0	1.8	1.9	1.8	0.5	0.3	0.4	0.9	2.1	3.0	O	36WA98	S
21	3.2	1.8	1.4	1.7	0.4	0.2	0.3	0.6	2.6	2.3	D	36WA99	Z
22	3.6	1.6	1.6	1.6	0.4	0.2	0.4	0.7	2.9	2.8	O	36WA99	Z
23	3.1	2.7	2.6	2.5	0.5	0.4	0.4	0.9	2.2	5.5	C	36BV24	A
24	3.8	2.2	2.2	2.3	0.4	0.2	0.5	0.9	2.9	Inc	C	36BV9	A
25	5.0	2.4	2.1	2.3	0.4	0.3	0.4	0.9	4.1	Inc	C	36BV24	A
26	3.5	2.2	2.0	2.2	0.4	0.3	0.4	0.9	2.6	Inc	F	33LI—	A
27	4.2	2.2	1.9	2.0	0.5	0.2	0.4	0.9	3.3	3.8	O	36BV6	A
28	2.8	2.0	1.8	2.0	0.3	0.2	0.4	0.9	1.9	2.0	D	36BV24	A
29	2.8	2.2	2.1	2.2	0.4	0.3	0.4	0.8	2.0	2.2	F	36BV24	A
30	3.6	2.4	2.5	2.4	0.4	0.3	0.4	0.9	2.7	3.6	O	36BV20	A
31	2.7	2.0	1.9	2.0	0.4	0.3	0.4	0.9	1.8	2.3	O	36BV24	A
32	3.3	2.2	2.1	2.1	0.5	0.3	0.5	0.8	2.5	3.2	?	36BV24	A
33	3.1	1.7	1.8	1.7	0.6	0.4	0.4	1.0	2.1	3.2	O	36BV4	A
34	2.5	1.8	1.4	1.8	0.4	0.3	0.3	0.8	1.7	1.6	D	36BV24	A
35	3.8	1.8	1.6	1.8	0.4	0.2	0.5	0.8	3.0	2.6	F	C-33MU34	B
36	3.0	2.0	2.0	2.0	0.4	0.2	0.4	0.7	2.3	2.9	O	36WA99	Z
Averages:													
	3.6	2.1	1.9	2.0	0.42	0.27	0.41	0.86	2.6	2.9			

3.2 is the average length of complete points.

Raccoon Corner Notched Points with Excurvate Blades

Type 2

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	3.2	2.2	1.8	2.3	0.4	0.2	0.5	0.8	2.4	2.6	C	46HK6	A
2	2.7	2.6	2.3	2.6	0.4	0.3	0.5	0.8	1.9	2.8	C	33AL61	B
3	3.2	2.6	2.4	2.6	0.6	0.3	0.7	0.9	2.3	4.6	C	C-33MU34	B
4	3.3	2.7	2.4	2.7	0.5	0.3	0.6	0.9	2.4	4.2	C	C-33MU34	B

APPENDIX I—*Continued.*

Raccoon Corner Notched Points with Excurvate Blades

Type 2

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
5	2.7	2.5	2.0	2.5	0.4	0.2	0.5	0.9	1.8	2.9	C	C-33MU34	B
6	4.6	2.7	2.5	2.8	0.4	0.2	0.6	0.9	3.7	6.6	C	C-33MU34	B
7	4.7	2.5	1.8	2.5	0.4	0.2	0.5	0.9	3.8	Inc	C	C-33MU34	B
8	3.2	2.6	1.7	2.6	0.5	0.3	0.4	0.8	2.4	3.8	O	36BV23	A
9	4.2	2.7	2.2	2.7	0.4	0.3	0.4	1.0	3.2	6.0	C	36BV25	A
10	4.7	2.4	1.9	2.3	0.4	0.2	0.5	0.9	3.8	Inc	C	36BV20	A
11	4.2	2.2	1.8	2.2	0.4	0.2	0.5	1.0	3.2	Inc	C	36BV25	A
12	4.3	2.5	2.2	2.5	0.5	0.2	0.4	1.0	3.3	Inc	C	36BV11	A
13	4.8	2.5	2.2	2.5	0.4	0.2	0.7	0.9	3.9	Inc	C	36BV25	A
14	3.8	2.2	1.5	2.2	0.4	0.2	0.5	0.8	3.0	3.0	O	36WA98	S
15	3.2	2.3	2.2	2.3	0.5	0.3	0.6	1.0	2.2	3.7	O	36WA98	S
16	2.4	2.0	1.7	2.0	0.5	0.3	0.3	0.7	1.7	2.0	D	36WA99	Z
17	3.2	2.0	1.8	2.0	0.4	0.2	0.5	0.8	2.4	3.1	O	36WA99	Z
18	2.5	2.0	1.7	2.0	0.4	0.3	0.5	1.0	1.5	2.3	O	36WA98	S
19	4.2	2.9	1.9	2.9	0.4	0.3	0.5	0.9	3.3	6.0	O	36WA94	Z
20	3.7	2.3	2.2	2.3	0.4	0.2	0.6	0.9	2.8	Inc	O	36WA99	Z
21	3.9	2.5	2.0	2.2	0.5	0.2	0.6	0.9	1.6	Inc	O	36WA99	Z
22	4.1	2.7	1.8	2.3	0.4	0.2	0.4	1.0	3.1	Inc	O	36WA95	Z
23	4.1	2.1	1.7	2.1	0.4	0.2	0.5	1.0	3.1	Inc	O	36WA99	Z
24	4.3	2.5	2.0	2.4	0.4	0.3	0.6	0.7	3.7	Inc	C	C-33MU34	B
25	3.2	2.4	1.8	2.4	0.4	0.2	0.5	0.7	2.5	Inc	F	C-33MU34	B
Averages:													
	3.8	2.4	2.0	2.4	0.43	0.22	0.52	0.88	2.7	3.7			

3.3 is the average length of complete points.

Raccoon Pentagonal Side Notched Points

Type 3

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	3.8	2.2	1.9	2.2	0.5	0.3	0.4	0.9	2.9	Inc	O	36WA31	S
2	3.5	2.2	2.0	2.2	0.4	0.3	0.5	0.8	2.1	Inc	O	36WA29	S
3	3.5	2.2	1.9	2.2	0.5	0.3	0.5	0.9	2.6	3.8	D	36WA98	S
4	2.5	2.0	1.6	2.0	0.3	0.2	0.4	0.7	1.8	1.4	O	36WA99	Z
5	2.5	2.3	2.0	2.3	0.5	0.3	0.5	0.7	1.8	2.5	O	36WA96	S
6	2.2	2.2	1.8	2.2	0.4	0.2	0.5	0.7	1.5	1.6	O	36BV24	A
7	3.1	2.6	2.3	2.5	0.4	0.3	0.5	1.1	2.0	3.3	C	46HK6	A
8	2.8	1.9	1.8	1.9	0.5	0.2	0.3	0.8	2.0	2.2	C	36BV24	A
9	3.2	2.2	2.0	2.2	0.4	0.2	0.5	1.0	2.2	3.0	D	36BV24	A
10	2.2	1.9	2.2	1.9	0.4	0.3	0.4	0.7	1.5	2.0	C	36BV24	A
11	2.9	2.1	2.2	2.1	0.4	0.3	0.3	0.8	2.1	2.8	C	C-33MU34	B
12	2.9	1.8	1.8	1.9	0.4	0.2	0.4	0.7	2.2	2.3	C	C-33MU34	B
13	2.5	1.8	1.8	1.8	0.4	0.2	0.4	0.8	1.7	1.7	O	36WA99	Z
14	2.9	2.2	2.4	2.2	0.4	0.2	0.4	0.9	2.0	2.5	F	C-33MU34	B
15	2.9	2.5	2.0	2.3	0.5	0.2	0.4	1.1	1.8	3.3	O	36AL16	B
Averages:													
	2.9	2.1	2.0	2.1	0.4	0.25	0.4	0.84	2.0	2.2			

2.8 is the average length of complete points.

Raccoon Pentagonal Corner Notched Points

Type 4

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	2.9	2.3	1.6	2.3	0.5	0.3	0.5	0.7	2.2	3.7	O	36BV24	A
2	2.5	3.0	2.4	3.0	0.5	0.2	0.6	0.8	1.7	3.9	C	46HK34	A
3	3.8	2.8	2.4	2.9	0.4	0.2	0.7	0.9	2.9	4.9	C	33LI—	A
4	2.0	1.8	1.3	1.7	0.4	0.2	0.4	0.7	1.3	1.5	O	36WA95	Z

APPENDIX I—*Continued.*

Raccoon Pentagonal Corner Notched Points

TYPE 4

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
5	3.9	2.3	1.9	2.3	0.4	0.2	0.5	0.8	3.1	Inc	C	36BV111	A
6	2.1	2.0	1.8	2.2	0.41	0.2	0.5	0.7	1.4	1.6	C	36BV4	A
7	3.0	2.0	1.9	2.3	0.55	0.21	0.35	0.7	2.3	Inc	O	36WA99	Z
8	3.1	2.0	2.0	2.3	0.5	0.3	0.4	0.8	2.3	Inc	O	36WA99	Z
Averages:													
	2.9	2.3	1.9	2.4	0.46	0.23	0.49	0.76	2.2	3.1			

2.7 is the average length of complete points.

Raccoon Side and Corner Notched Points on Straight Blades

TYPE 5

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	2.8	2.0	2.2	2.0	0.5	0.3	0.5	0.8	2.0	2.0	O	36WA99	Z
2	2.2	2.0	1.9	2.0	0.4	0.3	0.4	0.7	1.5	1.8	O	36WA90	S
3	2.5	1.8	2.0	1.8	0.4	0.2	0.4	0.7	1.8	2.0	O	36WA29	S
4	3.5	1.7	1.9	1.7	0.4	0.2	0.2	0.7	2.8	2.6	F	36BV24	A
5	1.7	2.0	1.7	2.0	0.4	0.3	0.3	0.8	0.9	2.1	C	36BV24	A
6	2.4	1.9	2.1	1.9	0.3	0.2	0.3	0.7	1.7	Inc	C	36BV24	A
7	2.5	2.0	2.1	2.0	0.4	0.2	0.4	0.6	1.9	2.1	O	36BV25	A
8	3.2	2.3	2.1	2.3	0.5	0.2	0.5	0.8	2.4	3.3	O	36WA31	S
Averages:													
	2.6	2.0	2.0	2.0	0.41	0.23	0.38	0.72	1.9	2.3			

2.6 is the average length of complete points.

Strike-A-Lights

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	2.2	2.3	2.0	2.1	0.7	0.4	0.2	0.8	1.4	3.0	O	36WA99	Z
2	2.2	1.8	2.1	1.8	0.6	0.3	0.3	1.1	1.1	2.3	O	36WA99	Z
3	1.8	1.6	2.1	1.8	0.4	0.2	0.3	0.8	1.0	1.8	O	36BV24	A
4	2.0	1.7	1.5	1.7	0.5	0.3	0.3	0.7	1.0	1.8	O	36WA98	S
5	2.2	1.7	1.8	1.7	0.5	0.3	0.3	0.8	1.4	2.3	O	36WA98	S
6	2.0	1.8	1.5	1.8	0.55	0.4	0.3	1.2	1.4	2.0	O	36WA99	Z
7	1.5	2.0	1.6	2.0	0.4	0.29	0.4	0.9	0.6	1.3	O	36WA29	S
8	1.9	2.3	2.1	2.3	0.5	0.4	0.4	0.8	1.1	Inc	O	36WA99	Z
Averages:													
	1.98	1.9	1.84	1.9	0.52	0.32	0.31	0.89	1.13	2.07			

2.0 is the average length of complete strike-a-lights.

End Scraper

AL	L	W	BW	SW	MT	BT	DN	SL	BL	Wt	LM	SN	C
1	2.3	1.8	1.5	1.7	0.4	0.3	0.3	1.0	1.3	2.0	O	36WA99	Z
2	2.5	2.2	2.1	2.0	0.6	0.3	0.5	1.1	1.4	3.3	O	36BV9	A
3	2.1	1.6	1.1	1.5	0.4	0.3	0.2	0.7	1.4	1.5	O	36WA98	S
4	2.0	2.1	2.0	2.1	0.4	0.3	0.4	1.0	1.0	2.0	O	36BV24	A
5	2.0	1.7	1.9	1.9	0.4	0.3	0.3	0.8	1.2	1.5	O	36BV24	A
Averages:													
	2.2	1.9	1.7	1.8	0.45	0.3	0.34	0.92	1.3	2.1			

APPENDIX II

Middle Woodland Site Survey Within 24 Upper Ohio Valley Counties in New York and Pennsylvania

General Recapitulation of Information

502 sites are Middle Woodland.
160 sites have triangular points and Raccoon Notched points.
66 sites have only Raccoon Notched points.
65 mounds are in western Pennsylvania.
12 mounds are in western New York.
39 sites have Bennington Corner Notched points.
21 sites have Bennington and triangular points.
19 sites have Bennington and Raccoon Notched points.
12 sites have Bennington, triangular, and Raccoon Notched points.
236 sites have Raccoon Notched points.
212 sites have triangular points.
6 sites have Garvers Ferry Corner Notched points.
8 sites have Kiski Notched points.
6 sites have Murphys Stemmed points.
5 sites have Garvers Ferry and Kiski Notched points.
2 sites have Garvers Ferry and Murphys Stemmed points.
5 sites have Kiski Notched and Murphys Stemmed points.
2 sites have Kiski Notched, Garvers Ferry and Murphys Stemmed points.

Mounds and Total Number of Sites
Listed by Counties

No.	County	Abbr.	No. of Mounds	No. of Sites
1	Allegheny	AL	6	19
2	Armstrong	AR	1	24
3	Beaver	BV	2	34
4	Butler	BT	1	19
5	Cambria	CB	0	3
6	Cattaraugus, NY	CA	6	22
7	Chautauqua, NY	CH	6	20
8	Clarion	CL	0	10
9	Crawford	CW	2	30
10	Elk	EL	0	1
11	Erie	ER	4	22
12	Fayette	FA	1	9
13	Forest	FO	0	3
14	Greene	GR	2	25
15	Indiana	IN	0	29
16	Jefferson	JE	0	6
17	Lawrence	LR	4	9
18	McKean	MC	1	1
19	Mercer	ME	1	11
20	Somerset	SO	0	6
21	Venango	VE	0	15
22	Warren	WA	17	24
23	Washington	WH	19	47
24	Westmoreland	WM	4	113
		Totals	77	502

Abbreviations

RN = Raccoon Notched, TP = Triangular Points, BP = Bennington Points, M = Mounds, GF = Garvers Ferry, KN = Kiski Notched, MS = Murphys Stemmed, X = Occurrence, XX = Heavy Concentration.

Major Raccoon Notched Point Sites Within 24 Upper Ohio Valley Counties in New York and Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36ER31	Melnick #1	Waterford	XX	X					
36ER181	Melnick #2	Waterford	XX	X					
30CA70	Zawatski #2	Salamanca	XX	X					

APPENDIX II—*Continued*

Major Raccoon Notched Point Sites Within 24 Upper Ohio Valley Counties in New York and Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
30CA93	Zawatski #23	Salamanca	XX	X					
C-30CA25	Kipp Island	Steamburg	XX	X					
C-30CH9	Kiantone	Jamestown	XX	X					
C-30CH25	Bemus Point	Chautauqua	XX	X					
36WA99	Buckaloons #10	Youngsville	XX	X					
36WA98	Buckaloons #9	Youngsville	XX	X					
36WA87	Harrington #2	Youngsville	XX	X					
36LR3	Edinburg	Edinburg	XX	X					
36LR21	Batinger	Edinburg	XX	X					
36BV24	Outdoor Theater	Aliquippa	XX	X	X				
36FA217	Stanish	Uniontown	XX	X					
36IN177	Elkin #4	Clymer	XX	X					
36WH921	Cowden #2	Prosperity	XX		X				
36LR102	Ashton Cemetery	Edinburg	XX	X					
		Total 17							

Sites Having Garvers Ferry Corner Notched, Kiski Notched, and Murphys Stemmed Points

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36AL19	Blawnox	Braddock		X			X	X	
36AR129	Murphy's Old House	Freeport					X	X	X
36AR19	Rosston	Leechburg					X	X	
36AR20	Heilman	Leechburg						X	X
36BV24	Outdoor Theater	Aliquippa	X	X	X		X	X	
36BV68	Coble Farm	Midland			X		X	X	X
36WM140	Thomas Orr	Greensburg						X	X
36WM23	Ryan	Slickville						X	X
36WM30	Garvers Ferry	Freeport					X		
36VE11	Franklin Point	Franklin		X					X
		Total 10							

Sites Having the Bennington Corner Notched Point and Other Associated Points

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36BV24	Outdoor Theater	Aliquippa	X	X	X		X	X	
36GR73	Biel #2	Mather		X	X				
36GR116	Hillman Land Co.	Mather			X				
36GR148	Whitlatch #3	Rogersville		X	X				
36GR160	Throckmorton #1	Rogersville		X	X				
36GR114	Heath Cliff (Crouse)	Waynesburg		X	X				
36WH825	Stopka #2	Ellsworth	X	X	X				
36WH796	Curtis McGaughey #2	Washington W.	X		X				
36WH786	Kiger #2	Ellsworth	X	X	X				
36WH798	Weaver Miles	Ellsworth	X	X	X				
36WH809	Shidler #1	Ellsworth	X	X	X				
36WH813	Shidler Village	Ellsworth	X	X	X				
36WH764	W. Dunn #34	Ellsworth			X				
36WH767	Fitzwater #28	Ellsworth			X				
36WH770	Gialata	Ellsworth			X				
36WH782	Howard M. Keys	Ellsworth	X	X	X				
36WH785	Kiger #1	Ellsworth	X	X	X				
36WH810	Shidler #2	Ellsworth	X	X	X				
36WH829	Ulery #4	Ellsworth	X		X				
36WH824	Stopka #1	Ellsworth	X	X	X				
36WH744	Bennett 27 #1	Ellsworth			X				
36WH443	Myles Site	Ellsworth			X				
36WH873	Chaffon #1	Amity		X	X				
36WH1044	Chaffon #2	Amity			X				

APPENDIX II—*Continued*

Sites Having the Bennington Corner Notched Point and Other Associated Points

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36WH1045	Chaffon #3	Amity			X				
36WH351	M. S. #41	W. Middletown		X	X				
36WH844	Mike Krajacic	W. Middletown		X	X				
36WH438	Bennington #1	Ellsworth		X	X				
36WH763	Rollo Dunn	Ellsworth		X	X				
36WH921	Cowden #2	Prosperity	XX		X				
36WH922	Robert Dunn	Prosperity			X				
36WH473	Krajacic Camp	W. Middletown	X		X				
36WH741	Bamberger #1	Amity	X	X	X				
36WH742	Bamberger #2	Amity	X	X	X				
36WH853	Taggert (Helsel #2)	Washington W.	X		X				
36WH662	Krajacic	W. Middletown			X				
36WH11	Smith Farm	Amity	X		X				
36WH943	McGaughey #2	W. Middletown	X		X				
36GR171	Rosemont Cemetery	Rogersville			X				
		Total 39 sites							

MIDDLE WOODLAND SITES LISTED BY COUNTIES WITHIN THE UPPER OHIO VALLEY IN NEW YORK AND PENNSYLVANIA

Allegheny County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36AL6	McKees Rocks (Mound)	Pittsburgh W.		X		X			
36AL19	Blawnox	Braddock	X	X			X		
36AL28	Bridgeville (Mound)	Bridgeville				X			
36AL50	Freed #2	Bridgeville	X						
36AL64	Crestoff Farm	Bridgeville	X	X					
36AL33	Guffey	Donora	X	X					
36AL43	Covert	Pittsburgh E.	X	X					
36AL61	Upper Leetsdale	Ambridge		X					
36AL259	Old Scout Camp	Ambridge	X						
36AL7	Leetsdale	Ambridge	X	X					
36AL47	Forward School	Monongahela	X	X					
36AL158	Kloiber	Baden	X	X					
36AL202	Bear Run	Emsworth	X						
36AL153	Williams	Glassport	X						
36AL69	Linhart	Glassport	X	X					
36AL96	Anderson Mound	New Kensington W.	X			X			
36AL272	Darlington Mound	Pittsburgh E.				X			
36AL83	Oakmont Mound	New Kensington W.				X			
36AL271	Peter Creek Mound	Glassport				X			
		Totals: 19 sites	13	10	0	6	1	0	0

Armstrong County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36AR4	Murphys Bottom	Freeport		X					
36AR9	Armstrong Run	Rimersburg	X						
36AR23	Martin	Distant							
36AR41	Smeltzer	Rural Valley	X	X					
36AR68	Bohan	Rural Valley							
36AR70	Bachlor	Mosgrove							
36AR95	Taxes	Worthington		X					
36AR105	Worthington	Worthington		X					
36AR119	Wattersonville (Mound)	East Brady	X	X		X			
36AR136	Hogg	Worthington	X						
36AR140	Rural Valley #1	Rural Valley		X					

APPENDIX II—*Continued*

Armstrong County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36AR142	Wilson	Rural Valley	X	X					
36AR145	Fleming	Rural Valley	X	X					
36AR148	Boyer I	Rural Valley	X						
36AR150	Bohan	Rural Valley							
36AR162	Croyle Farm	Elderton		X					
36AR183	Smeltzer	Rural Valley		X					
36AR199	West Ford	Kittanning							
36AR208	Bark #5	Elderton	X	X					
36AR221	G. Kimmel #5	Elderton	X	X					
36AR146	Coulter	Rural Valley		X					
36AR129	Murphy's Old House	Freeport					X	X	X
36AR19	Rosston	Leechburg					X	X	
36AR20	Heilman	Leechburg						X	X
		Totals: 24 sites	9	13	0	1	2	3	2

Beaver County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36BV2	Vanport	Beaver	X	X					
36BV24	Outdoor Theater	Aliquippa	XX	X	X		X	X	
36BV23	Hills Plaza	Aliquippa	X	X					
36BV26	Kochanioski	Aliquippa	X	X					
36BV28	Camp	Zelienople	X						
36BV37	Wassler #3	Aliquippa							
36BV39	McMichaels	Aliquippa	X	X					
36BV50	New Barn	Beaver							
36BV59	Truck Farm	Beaver	X						
36BV68	Coble Farm	Midland					X	X	X
36BV70	Rossomme	Midland							
36BV77	Darlington Lake	New Galilee							
36BV78	Parish Farm	Aliquippa	X	X					
36BV88	Murdocksville	Clinton							
36BV111	South Service Creek	Aliquippa	X						
36BV118	Muntzel	Aliquippa	X						
36BV137	Toogood Site	Clinton							
36BV144	Upper Georgetown	Midland	X	X					
36BV158	Clyde	Zelienople	X						
36BV160	Plaza West	Aliquippa	X	X					
36BV176	Muntzel #3	Aliquippa							
36BV180	Belich Farm	Aliquippa	X	X					
36BV195	Feyke Field	New Galilee	X						
36BV197	Veon	New Galilee							
C-36BV243	Brick Kiln Overlook	Beaver	X						
36BV60	Phillis Island	Hookstown	X	X					
36BV6	Glasgow	E. Liverpool	X	X					
36BV13	Circle	Aliquippa	X						
36BV20	Wilson Triangle	Aliquippa	X	X					
36BV64	D. C. Bonzo	Baden	X	X					
36BV9	Ohioview	Midland	X	X		X			
36BV25	Dead End	Aliquippa	X	X					
C-36BV229	Crucible Steel	Hookstown	X	X					
C-36BV250	Stone House Mound	Midland				X			
		Totals: 34 sites	24	16	1	2	2	2	1

Butler County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36BT13	Hartman Lake	Evans City							
36BT78	Stamm School	Evans City	X						

APPENDIX II—*Continued*

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36BT105	Grote Site	Evans City	X						
36BT16	John Nesbitt	Zelienople							
36BT17	David Nesbitt	Zelienople	X						
36BT23	Dutilh	Mars	X						
36BT110	Strawberry Run	Mars							
36BT25	Old McCoy	Slippery Rock	X						
36BT82	College Site	Slippery Rock		X					
C-36BT177	Hogg	Slippery Rock	X						
36BT72	Love Site	Valencia	X	X					
366BT109	Harvey Strain	Valenica							
36BT112	Sewage Plant	Baden	X						
36BT118	Radio Tower	West Sunbury	X						
36BT139	Jones #4	Saxonburg							
36BT141	Wiley (A)	Saxonburg							
36BT156	Szebalski #1	Curtisville		X					
36BT161	Schilling #1	Butler		X					
C-36BT184	Airport Mound	Butler				X			
		Totals: 19 sites	9	4	0	1	0	0	0

Cambria County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36CB3	Settlemeyer #2	Ebensburg		X					
36CB6	Dalton Run	Rachelwood							
36CB141	Topper Farm	Geistown	X						
		Totals: 3 sites	1	1	0	0	0	0	0

Cattaraugus County, New York

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
30CA70	Zawatski #2	Salamanca	XX	X					
30CA74	Zawatski #6	Salamanca	X	X					
30CA93	Zawatski #23	Salamanca	XX	X					
30CA10	Cold Spring	Red House	X	X		X			
30CA25	Kipp Island	Steamburg	XX	X					
30CA107	State Line Run	Steamburg	X	X					
30CA73	Killbuck Mound	Salamanca				X			
30CA68	Gerry Johnson	Steamburg	X	X					
30CA12	Cold Spring #1	Red House		X					
30CA44	Twin Bridge	Red House	X	X					
30CA30	Sawmill Run	Steamburg	X	X					
30CA100	Sawmill Run South	Steamburg				X			
30CA6	Quaker Bridge	Steamburg	X	X					
30CA26	Quaker Run South	Steamburg	X	X					
30CA67	Mound Site	Randolph				X			
30CA34	Onoville Store	Steamburg	X	X					
30CA32	Orth Site	Steamburg	X	X					
30CA29	Dick Rapp	Steamburg		X					
30CA27	Knob Hill	Steamburg	X	X					
30CA9	Old Town Road	Steamburg	X						
30CA115	Vandalia Mound #1	Knapp Creek				X			
30CA116	Vandalia Mound #2	Knapp Creek				X			
		Totals: 22 sites	15	16	0	6	0	0	0

Chautauqua County, New York

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
C-30CH8	Kiantone I	Jamestown	X	X					
C-30CH9	Kiantone II	Jamestown	XX	X					

APPENDIX II—*Continued*

Chautauqua County, New York

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
C-30CH25	Bemus Point	Chautauqua	XX	X		X			
C-30CH27	Mound Site	Chautauqua				X			
C-30CH43	Bonnybrook	Chautauqua	X	X					
C-30CH48	Prendergast Point	Chautauqua	X	X					
C-30CH46	Power Boat Site	Chautauqua		X					
C-30CH35	Goose Creek	Lakewood							
C-30CH34	Loomis Garden	Lakewood							
C-30CH38	Ashville Bay	Lakewood							
C-30CH72	Carlson I	Lakewood							
C-30CH52	Johnson II	Cassadaga		X					
C-30CH53	Johnson III	Cassadaga							
C-30CH59	Ames	Cassadaga		X					
C-30CH78	Anderson Farm	Kennedy	X	X					
C-30CH85	Poland Center Mound	Gerry				X			
C-30CH86	Poland Village	Gerry							
C-30CH87	Morton Mound	Panama				X			
C-30CH88	Whitney's Mound	Chautauqua				X			
C-30CH89	Billing's Mound	Chautauqua				X			
		Totals: 20 sites	6	9	0	6	0	0	0

Clarion County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36CL33	McFarland Site	Rimersburg		X					
36CL34	Wilson Site #1	Rimersburg							
36CL38	Bullock's Crossing	Knox	X						
36CL42	Licking Creek	Rimersburg	X	X					
36CL47	Simpson Site #3	Knox	X						
36CL50	Wheeter Site	Rimersburg	X	X					
36CL51	Lobaugh Site	Knox	X						
36CL54	Courson Site	Rimersburg							
36CL92	Cherico Site	New Bethlehem							
36CL66	Slaugenhaup Site	Rimersburg		X					
		Totals: 10 sites	5	4	0	0	0	0	0

Crawford County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36CW4	Danner Mound	Lake Canadohta				X			
36CW21	Propagation #57	Geneva							
36CW9	Kebort	Geneva							
36CW162	Hotson Farm A	Geneva	X	X					
36CW248	Peterson #5	Geneva							
36CW259	Mook #1 & 2	Geneva	X						
36CW48	Brooks	Linesville							
36CW81	Steward—G	Linesville	X						
36CW91	Jablonski—B	Linesville							
36CW92	Bartges—A	Linesville	X	X					
36CW93	Zigafoose	Linesville							
36CW98	Gillette—B	Linesville	X	X					
36CW100	Ford Island	Linesville							
36CW6	Manny Threuret	Meadville							
36CW7	Hilgendorf Dairy	Meadville							
36CW173	Hall Farm #1	Meadville	X						
36CW175	Hall Farm #2	Meadville	X						
36CW104	Patterson	Hartstown	X						
36CW112	Bounded Site	Harmonsburg		X					
36CW115	Classic	Harmonsburg							

APPENDIX II—*Continued*

Crawford County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36CW118	Harvey—A	Cochranton	X						
36CW119	Harvey—B	Cochranton	X						
36CW120	Harvey—C	Cochranton	X						
36CW125	Custead—J	Cochranton	X	X					
36CW144	Hall #8	Cochranton	X	X					
36CW146	Hall #6	Cochranton							
36CW229	Preston #1	Cochranton							
36CW58	Nelson Mound	Cochranton				X			
C-36CW351	McEntire	Conneaut Lake	X						
36CW324	Burkett CB 22	Conneaut Lake	X						
		Totals: 30 sites	15	6	0	2	0	0	0

Elk County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36EL39	Medix Run	Weedville							
		Totals: 1 site	0	0	0	0	0	0	0

Erie County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36ER30	Nelson	Waterford	X	X					
36ER31	Melnick #1	Waterford	XX	X					
36ER32	Boleratz II	Waterford	X	X					
36ER33	Lewis I Site	Waterford	X	X					
36ER19	Boleratz I	Waterford	X	X					
36ER24	Perry Troyer Site	Waterford	X	X					
36ER26	Wise Mound	Waterford				X			
36ER34	Wheeler Site	Waterford		X					
36ER48	Indian Head Mound	Waterford				X			
36ER96	Wheeler Cache Site	Waterford							
36ER181	Melnick #2	Waterford	XX	X					
36ER182	Kingen #1	Waterford	X	X					
36ER185	Kingen #4	Waterford	X	X					
36ER186	Kingen #5	Waterford	X	X					
36ER187	Kingen #6	Waterford	X	X					
36ER195	Dollar #4	Waterford	X	X					
36ER196	Dollar #5	Waterford	X	X					
36ER198	Dollar #7	Waterford	X	X					
36ER203	Port #1	Waterford	X	X					
36ER207	Graham #1	Union City	X	X					
C-6ER220	Mystic Mound	Millers Station				X			
36ER16	Clouna Mound	Spartansburg				X			
		Totals: 22 sites	16	17	0	4	0	0	0

Fayette County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36FA51	Horse Shoe Bend	Confluence							
36FA53	Croushore Farm	Carmichaels	X	X					
36FA191	Bradisch—3	Connellsville							
36FA205	Binotto—2	Dawson							
36FA210	Haas	Dawson							
36FA217	Stanish	Uniontown	XX	X					
36FA231	M. Speers	Fayette City							
36FA275	Harim #1	Uniontown							
36FA229	Blosser Mound	Morgantown N.				X			
		Totals: 9 sites	3	2	0	1	0	0	0

APPENDIX II—*Continued*

Forest County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36FO1	Siggins	West Hickory	X	X					
366FO2	Hunter Station	President	X	X					
36FO17	Schwab Run	West Hickory	X	X					
		Totals: 3 sites	3	3	0	0	0	0	0

Greene County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36GR4	Horn Farm	Mather							
36GR21	Fisher Site	Majorsville							
36GR66	The Whipkey Site	Carmichaels	X						
36GR71	Thomas No. 1	Carmichaels	X	X	X				
36GR102	Delphine Game Land	New Freeport							
36GR140	Hillman Coal & Coke	Rogersville	X						
36GR160	Throckmorton #1	Rogersville	X	X					
36GR171	Rosemont Cemetery	Rogersville			X				
36GR175	Tressel	Holbrook							
36GR63	Gensler	Waynesburg	X						
36GR36	Crow Mounds 1 & 2	Majorsville				X			
36GR49	Mackey Farm	New Freeport							
36GR73	Biel #2	Mather		X	X				
36GR76	Lost Leah	Carmichaels	X	X					
36GR179	Freeman	Wadestown, WV-PA							
36GR111	Hawkins #1	Ellsworth							
36GR116	Hillman Land Co.	Mather			X				
36GR126	Weaver	Mather							
36GR129	Neil Corner	Carmichaels							
36GR148	Whitlatch #3	Rogersville		X	X				
36GR160	Throckmorton #1	Rogersville		X	X				
C-36GR180	Mapleton Mound	Masontown				X			
36GR161	Throckmorton #2	Rogersville							
36GR175	Tressel Site	Holbrook							
36GR114	Heath Cliff (Crouse)	Waynesburg		X	X				
		Totals: 25 sites	6	7	6	2	0	0	0

Indiana County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36IN22	Wilbur Bell	Elderton	X	X					
36IN25	Wissinger Farm	Elderton	X	X					
36IN290	Flint Knob	Elderton	X	X					
36IN29	Hamil Farm	Ernest	X	X					
36IN283	Ken Adams #3	Ernest	X	X					
36IN37	Weaver	Valier	X						
36IN41	West Mahoning #3	Dayton		X					
36IN47	Stiteler #1	Plumville							
36IN291	Leisure Run	Plumville	X	X					
36IN111	Griffith Site	Indiana							
36IN113	W. A. George #1	Indiana	X						
36IN122	Ralph Brown	Indiana	X	X					
36IN133	Shopping Mart	Indiana	X						
36IN139	Delton Stiles	Indiana	X	X					
36IN161	Yellow Creek #1	Brush Valley	X	X					
36IN168	Yellow Creek #8	Brush Valley	X	X					
36IN194	Blacklick Church	Vintondale	X	X					
36IN216	Campbell #1	Bolivar							
36IN223	Penrose #2	Bolivar							
36IN287	Grafton #1	Bolivar							

APPENDIX II—*Continued*

Indiana County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36IN255	Mears #2	Clymer	X	X					
36IN260	Zubalik #2	Clymer	X	X					
36IN265	Martin	Clymer		X					
36IN274	Elkin #1	Clymer	X						
36IN277	Elkin #4	Clymer	XX	X					
36IN278	Greene #1	Clymer							
36IN279	Greene #2	Clymer	X						
36IN115	Overman	Clymer	X						
36IN319	Clawson	Blairsville	X	X					
		Totals: 29 sites	22	17	0	0	0	0	0

Jefferson County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36JE15	Jack Hall	Summerville							
36JE41	Montgomery Farm #3	Summerville							
36JE51	Shaffer Site	Summerville							
36JE85	Robert Johns	Summerville							
36JE21	Hamilton #3	Valier	X						
36JE34	Hamilton #2	Valier							
		Totals: 6 sites	1	0	0	0	0	0	0

Lawrence County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36LR3	Edinburg (Mound)	Edinburg	XX	X		X			
36LR11	Chambers (Mound)	Edinburg	X	X		X			
36LR76	Weinschenk's Island	Bessemer	X						
36LR98	Westminster College	New Castle N.							
36LR1	West Pittsburgh	New Castle		X					
36LR5	Morrow Place	New Castle	X	X		X			
36LR21	Bollinger Site	Edinburg	XX	X					
36LR10	Young Mound	New Castle N.				X			
36LR102	Ashton Cemetery	Edinburg	XX	X					
		Totals: 9 sites	6	6	0	4	0	0	0

McKean County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
C-36MC14	Nelse Run Mound	Cornplanter Run				X			
		Totals: 1 site	0	0	0	1	0	0	0

Mercer County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36ME16	Stewart I	Sharpsville							
36ME51	Stewart Farm	Sharpsville							
36ME62	Seven Acres	Sharpsville							
36ME31	Hitchcock #11	Greenville							
36ME107	Spring	Mercer							
36ME108	Route 58	Mercer							
36ME114	Irish Town	Mercer	X	X					
36ME176	Arden Rice #1	Mercer	X						
36ME177	Arden Rice #2	Mercer	X	X					
36ME136	McDougal Farm #1	Grove City							
36ME58	Sandy Lake Mound	Sandy Lake				X			
		Totals: 11 sites	3	2	0	1	0	0	0

APPENDIX II—*Continued*

Somerset County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36SO15	Holfsopple	Hooversville	X	X					
36SO19	Dock	Friendsville							
36SO20	Big Crossing	Ohiopyle		X					
36SO108	Moser #3	Meyersdale							
36SO129	Groff #2	Confluence							
36SO160	Berkey #2	Somerset							
		Totals: 6 sites	1	2	0	0	0	0	0

Venango County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36VE4	West Sandy Site	Kennerdell		X					
36VE3	Eagle Rock Village	President		X					
36VE2	President Village	President		X					
36VE23	Venango Manor #3	Utica		X					
36VE50	Seneca Farm	Oil City	X	X					
36VE69	Oleopolis Village	President		X					
36VE124	Polk Farm	Polk	X	X					
36VE182	Burkhart Farm	Utica							
36VE156	Triple Oak	Kennerdell							
36VE12	Pithole Creek	Pleasantville	X	X					
36VE14	Seneca Run	Franklin	X	X					
36VE16	Martin-Harvey	Utica	X						
36VE25	Husk	Utica							
36VE28	Jackson's Eddy	Emlenton	X	X					
36VE11	Franklin Point	Franklin		X					X
		Totals: 15 sites	6	11	0	0	0	0	1

Warren County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36WA99	Buckaloons #10	Youngsville	XX	X					
36WA98	Buckaloons #9	Youngsville	XX	X		X			
36WA29	Irvine #3	Youngsville	X	X					
36WA31	Irvine #1	Youngsville	X	X					
36WA96	Buckaloons #6	Youngsville	X	X		X			
36WA97	Buckaloons #8	Youngsville	X	X					
36WA2	Sugar Run	Cornplanter	X	X		X			
36WA87	Harrington #2	Youngsville	XX	X		X			
36WA80	Ziegler	Tidioute							
36WA1	Williams Mound	Russell				X			
36WA15	Berkabile #1	Cornplanter Run	X	X					
36WA93	Buckaloons #1	Youngsville	X	X		X			
36WA95	Buckaloons #5	Youngsville	X	X		X			
36WA102	Buckaloons #13	Youngsville	X	X		X			
36WA24	Langler Mound	Cornplanter Run				X			
36WA133	Gravel Test Site	Cornplanter Run							
C-36WA226	Cornplanter Mound 4	Cornplanter Run				X			
C-36WA227	Cornplanter Mound 1	Cornplanter Run				X			
C-36WA228	Cornplanter Mound 2	Cornplanter Run				X			
C-36WA229	Cornplanter Mound 3	Cornplanter Run				X			
C-36WA230	Cornplanter Mound 5	Cornplanter Run				X			
C-36WA231	Kinzua Beach Mound	Cornplanter Bridge				X			
C-36WA232	Irvine Mound 5	Youngsville				X			
C-36WA233	Harrington Mound	Warren				X			
		Totals: 24 sites	12	12	0	17	0	0	0

APPENDIX II—*Continued*

Washington County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36WH714	Meadows Mound Village	Washington E.		X		X			
36WH606	Opossum Run	Hackett							
36WH29	Riverview Mound	Monongahela				X			
36WH31	Fisher, Courtney Mound	Monongahela				X			
36WH721	Pollock's Hill Mound	Monongahela				X			
36WH415	Avella Mound	Avella			X	X			
36WH297	Meadowcroft	Avella							
36WH687	Lowry #5	Midway							
36WH707	Salvini Site	Midway							
36WH121	Abrutz Mound	Midway				X			
C-36WH973	Carter #3	Midway	X	X					
C-36WH999	C. V. Cowden	Midway							
C-36WH122	Lutheran Mound	Midway				X			
36WH605	West Alexander	Claysville							
36WH106, 110	Mungai Farm	Midway	X	X					
C-36WH965	Robertson #1	Claysville	X	X					
36WH411	Plumbsock	Prosperity							
36WH703	Bentz Mound	Prosperity				X			
C-36WH929	Sandberg #2	Prosperity		X					
C-36WH978	Pleasant Grove	Prosperity							
36WH11	Smith Farm	Amity	X		X				
36WH14	Moore Farm	Amity	X	X					
36WH435	Winnett	Amity	X	X					
36WH594	J. B. Wilson	Amity							
36WH596	G. Earnest	Amity		X					
36WH742	Evert Bamberger	Amity	X	X	X				
36WH801	Abraham Phillips	Amity	X	X					
36WH804	Wilson Pizzi #2	Amity	X						
36WH616	Candor Mound	Clinton				X			
36WH40	Van Eman	Canonsburg		X					
36WH90	Log Cabin	Bridgeville	X						
36WH248	Hickman Barn	Bridgeville							
36WH477	Dunsfort	Bethany	X	X					
36WH725	Hunter Site	W. Middletown							
36WH974	Dunkle	W. Middletown							
36WH717	Hamilton Farm	Washington W.							
36WH727	Clarks Green Acres	Washington W.							
36WH732	Bartusiak	Washington W.							
36WH796	Curtis McGaughey #2	Washington W.	X		X				
36WH826	Alex Taggart	Washington W.	X						
36WH947	Munson	Washington W.	X						
C-36WH950	Lutz #3	Washington W.							
C-36WH975	Dixon	Washington W.	X	X					
36WH55	Tau Site	Washington W.							
36WH39	White Farm Mound	Washington W.				X			
36WH618	Bates #1	Washington W.							
36WH661	J. T. Hamilton	Washington W.							
36WH36	Linn Mound	Washington E.				X			
36WH37	Old Wylie Mound	Washington E.				X			
36WH456	Ballfield Site	Washington E.	X						
36WH632	Frank	Washington E.							
36WH640	Eighty Four	Washington E.							
36WH647	Clair	Washington E.	X						
36WH678	Hatfield	Washington E.	X	X					
36WH665	Mazur	Washington E.							
36WH675	Ashmore #2	Washington E.		X					
36WH873	Chaffon	Amity		X	X				

APPENDIX II—*Continued*

Washington County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36WH58	Hackney	Amity	X	X					
36WH265	John O'Brien	Amity							
36WH670	Old Zollarsville	Ellsworth							
36WH782	Howard M. Keys	Ellsworth	X	X					
36WH786	Kiger #2	Ellsworth	X	X	X				
36WH787	Kiger Pond	Ellsworth	X	X					
36WH798	Weaver Miles	Ellsworth	X	X	X				
36WH809	Shidler #1	Ellsworth	X	X	X				
36WH813	Shidler Village	Ellsworth	X	X	X				
36WH824	Stopka #1	Ellsworth	X	X	X	X			
36WH875	Fava #1	Ellsworth		X					
36WH885	H. B. Keys #1	Ellsworth	X	X					
36WH437	John Krupzig	Ellsworth	X	X					
36WH443	Myles	Ellsworth			X				
36WH601	Greenlee Camp Site	Ellsworth							
36WH80	S. PA. Railroad	Canonsburg							
36WH81	Hahn's Bench	Canonsburg		X					
36WH82	Hahn's	Canonsburg		X					
36WH301	Wiley Farm	Washington E.	X			X			
36WH764	W. Dunn #34	Ellsworth			X				
36WH767	Fitzwater #28	Ellsworth			X				
36WH770	Gialata	Ellsworth			X				
36WH774	Jim Greenlee #3	Ellsworth							
36WH782	Howard M. Keys	Ellsworth	X	X	X				
36WH785	Kiger #1	Ellsworth	X	X	X				
36WH800	Pershina #2	Clinton							
36WH810	Shidler #2	Ellsworth	X	X	X				
36WH825	Stopka #2	Ellsworth	X	X	X				
36WH829	Ulery #4	Ellsworth	X		X				
36WH832	Wayne Weaver #1	Amity		X					
36WH833	Wayne Weaver #2	Amity							
36WH876	Fava #2	Ellsworth							
36WH877	Fava #3	Ellsworth							
36WH880	Gas Light Bottom	Ellsworth							
36WH925	Beatty	Prosperity							
C-36WH946	Patton #1	W. Middletown							
C-36WH973	Carter #3	Midway	X	X					
C-36WH1010	J. Gagich	Avella				X			
C-36WH1028	Crall Mound	Monongahela				X			
36WH10	Pollocks Knob	Glassport				X			
36WH703	Bentz Mound	Prosperity				X			
36WH781	Indian Ridge Cairns	Ellsworth				X			
36WH744	Bennett Chapt. 27 #1	Ellsworth			X				
C-36WH1044	Chaffon #2	Amity			X				
C-36WH1045	Chaffon #3	Amity			X				
36WH351	M. S. #41	W. Middletown		X	X				
36WH844	Mike Krajacic	W. Middletown		X	X				
36WH438	Bennington #1	Ellsworth		X	X				
36WH763	Rollo Dunn	Ellsworth		X	X				
36WH921	Cowden #2	Prosperity	XX		X				
36WH922	Robert Dunn	Prosperity			X				
36WH473	Krajacic Camp	W. Middletown	X		X				
36WH741	Bamberger #1	Amity	X	X	X				
36WH853	Taggert (Helsel #2)	Washington W.	X		X				
36WH662	Krajacic (Lowery)	W. Middletown	X		X				
36WH943	McGaughey #2	W. Middletown	X		X				
		Totals: 113 sites	41	40	32	19	0	0	0

APPENDIX II—*Continued*

Westmoreland County, Pennsylvania

Site Number	Site Name	7.5′ USGS Map	RN	TP	BP	M	GF	KN	MS
36WM20	Summy	Mt. Pleasant		X					
36WM151	Thomas Hurst #3	Mt. Pleasant							
36WM522	Wilkinson	Mt. Pleasant	X						
36WM40	Herminie	Irwin	X	X					
36WM410	McGrew	Irwin		X					
36WM537	Blair Farm Mounds	Irwin				X			
36WM44	Hannas Run	Wilpen		X					
C-36WM666	Bear Cave Tower	Wilpen	X						
36WM50	Billy (Mound)	Donora				X			
36WM432	Caliagni #1	Donora							
36WM455	Backstrum #3	Donora							
C-36WM677	Billy #3	Donora							
36WM70	Shupe	Smithton	X	X					
36WM216	Rubright Farm Site	Murrysville							
36WM219	James Torrance #2	Murrysville							
36WM234	Speedway	Latrobe							
36WM237	Orgovan	Latrobe							
36WM264	Foul Air	Latrobe							
36WM299	Greenhouse #1	Latrobe							
C-36WM638	Clark	Latrobe	X						
36WM588	Stewart #2	Latrobe	X	X					
36WM245	Dillon	Mammoth							
C-36WM650	Conrath #1	Mammoth	X	X					
36WM249	Lenhart #1	Stahlstown	X						
36WM256	Scaife #4	Derry							
36WM477	Dividing Ridge	Derry							
36WM487	Bergman #4	Derry	X	X					
C-36WM622	Five Points Road #1	Derry	X						
36WM320	Frye	Blairsville							
36WM321	Keeno #2	Blairsville							
36WM359	Dumlap #4	Blairsville							
36WM523	Sulkosky #3	Blairsville	X						
36WM524	Miodufzeuski	Blairsville	X						
36WM287	Hillside #1	Derry	X	X					
36WM410	McGrew	Irwin							
36WM496	Andree #3	Avonmore							
36WM498	Andree #5	Avonmore	X	X					
36WM499	Andree #6	Avonmore	X	X					
36WM507	Lick Run	Rachelwood	X	X					
36WM573	Christopher #1	Saltsburg	X						
36WM580	Bortz #1	Saltsburg	X	X					
36WM596	Marcellus	Greensburg	X	X					
36WM30	Garvers Ferry	Freeport					X		
36WM140	Thomas Orr	Greensburg						X	X
36WM23	Ryan	Slickville						X	X
36WM39	Haymaker Run Mound	Murrysville				X			
36WM685	Shepler Mound	Donora				X			
		Totals: 47 sites	19	14	0	4	1	2	2

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DANIEL H. SANDWEISS

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PREFACE

The intent of this monograph is twofold. First, it is a site report for the Late Horizon (Inka, ca. A.D. 1480–1532) fishing site called Lo Demás, located on the north side of the Chincha valley on the south-central coast of Peru. Second, it is an exploration of late pre-Hispanic economic organization on the Peruvian coast, using ethnohistoric data to generate hypotheses and testing these hypotheses through archaeological excavation and analysis. Given these foci, the monograph is necessarily written for an audience of specialists in Andean studies. However, the results touch on areas of potentially wider interest, such as the recognition of specialization and status differences in the archaeological record, the interplay between ethnohistoric and archaeological data, the analysis of organic remains, etc. Therefore, I have attempted to make this study accessible to non-Andeanists, principally by defining terms used by specialists in the region. Spanish and Quechua terms are italicized, and definitions appear in parentheses or notes following the first use of each term. The glossary at the end of the monograph provides expanded definitions for these terms, for some place and proper names, and for other specialized terms in English.

All translations from Spanish to English are my own. The original Spanish texts for citations from colonial documents are provided in the notes. In the text, citations from colonial documents follow the usual convention of listing the year of the edition used in parentheses, the year of original publication or writing in brackets, the page number(s) for the edition used, and the chapter or other internal divisions of the original for cross-correlating with other editions.

Occasionally, tables or figures from other publications are cited. To avoid confusion with references to tables and figures in this monograph, I use the following convention: tables or figures which are listed *within* the same parentheses as a citation to another publication refer to that publication; tables or figures from this study are cited separately (with or without parentheses).

This monograph is a revised version of my doctoral dissertation (Sandweiss, 1989). Most of the original tables and illustrations are reproduced here; those which are omitted are referenced to the dissertation. Several of the tables have been modified to accommodate more recent data; such changes are noted in the text or notes.

I have benefitted from the assistance of many individuals and institutions (*see* Acknowledgments). However, all omissions, and errors of fact and interpretation are mine alone.

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ABSTRACT

At the time of the European invasion, the Chincha valley, Peru, was the seat of an important coastal polity under Inka dominion. The ethnohistoric record shows a prosperous kingdom with a far-flung trading network and a large, local population rigidly divided into occupationally specialized communities. Among the specialists were fishermen who, according to one document, lived in their own settlement and did nothing but fish, drink, and dance.

A section of the late pre-Hispanic Chincha fishing settlement described by the document was discovered and excavated during archaeological field work (1983–1984) designed to evaluate the ethnohistoric record for Chincha and assess the role of fishermen in late pre-Hispanic coastal economies. This monograph details work at this Late Horizon site, called "Lo Demás," and contrasts the archaeological data with the incomplete documentary record. Only common fishermen were rigidly specialized, and even they had to carry out the daily chores of domestic life in addition to fishing. In contrast, the lords of the fishermen controlled a variety of craft specialists as well as fishermen. Status differences in architecture and subsistence as well as other activities were well marked in the archaeological record. These findings corroborate more extensive ethnohistoric data from north coastal Peru, indicating an interregional dimension to late pre-Hispanic coastal economies.

In the documents concerning Chincha, the information on specialization refers specifically to the period of Inka domination of the coast, and not to pre-Inka conditions. Similarly, the excavations at "Lo Demás" provide evidence only for the Inka period economy; the absence of a pre-Inka component at the site is an important indicator of significant reorganization of the local Chincha economy by the Inka. However, a comparison of the Chincha data with north coast archaeological research shows that the principles of economic organization determined for the Chincha fishermen also were broadly characteristic of the pre-Inka, Late Intermediate Period Chimú kingdom. This, in turn, indicates that the Inka modified but did not originate the kind of economic organization that the ethnohistoric record describes for the Peruvian coast during the Late Horizon.

CHAPTER 1

INTRODUCTION

The ethnohistoric record for the Andes provides valuable insights into the economic, political, and social structures of the region's late pre-Hispanic inhabitants. Unfortunately, this record is neither complete nor infallible. The native informants and their European observers are long dead, and we cannot know what biases motivated them. However, the archaeological investigation of these peoples' material remains can, at the least, confirm or deny many specific aspects of the ethnohistoric record. At best, archaeology can provide a "contrasting portrayal of the past" (Charleton, 1981:155) leading to new insight into the Andean world on the eve of the European invasion in A.D. 1532.

This study concerns the economic organization of Chincha, an important coastal polity under Inka dominion at the time of the Spanish Conquest. The few ethnohistoric documents available for Chincha show a prosperous coastal kingdom with a far-flung trading network and a large, local population rigidly divided into occupationally specialized communities. Among the specialists, the primary document speaks most clearly and at greatest length about the fishermen, said to number 10,000 tribute-payers, or about a third of the total population. These fishermen lived apart in their own settlement and—when not fishing—enjoyed the finer aspects of pre-Columbian life, "drinking and dancing and so on" (Rostworowski, 1970:171).

This picture is an appealing one, but the archaeological record suggests that it is not the whole truth. Excavations in part of the Chincha fishing settlement indicate that only the common fishermen were rigidly specialized; even they had to carry out the daily chores of domestic life (an area not covered by the written record) in addition to fishing. In contrast, the lords of the fishermen controlled the production of a variety of crafts as well as of fish; this aspect of pre-Hispanic coastal organization is seen in the ethnohistoric record for the Peruvian north coast, but the ethnohistory for Chincha itself does not hint at such complexity. Although the document for Chincha mentions the existence of lords, it remained for the archaeology to show their different status in terms of architecture, subsistence, and organization of production.

The archaeology also shows that the section of the fishing settlement studied dates to the Late Horizon, or period of Inka domination of the Andes. The Inka originated in Cuzco, in the southern highlands of Peru; in the mid-1400s, they began a wave of conquest that rapidly spread their control for thousands of kilometers along the Andean mountain chain and adjacent territories. Chincha was incorporated into the Inka Empire around A.D. 1476 (Menzel and Rowe, 1966:67), probably by treaty rather than military defeat. Although previous studies have suggested that the Inka left the economic structure of Chincha largely intact (e.g., Rostworowski, 1970), this investigation suggests that the organization of Chincha *did* change significantly under Inka rule.

Objectives and Organization

The major objectives of this study are listed below in order of increasing generality. The first objective (necessary to the evaluation of the others) is the archaeological identification of the Late Horizon Chincha fishing settlement described by the documents. A portion of this settlement was found, named "Lo Demás," and partially excavated. The second objective is the delineation of the lifeways of the site's inhabitants, including subsistence, production, and exchange. Third is the evaluation of the archaeological data in terms of the document-derived models of economic organization. The final objective is a comparison with data on earlier coastal economies to determine the degree to which the ethnohistoric record reflects pre-Inka conditions and the degree to which it shows transformations wrought under Inka rule.

These objectives are intimately related to the ethnohistoric record for Chincha and for the late pre-Hispanic coast in general, but at the higher levels of generality, they transcend a mere confirmation or denial of statements made in specific documents. Rather, I hope to contribute to an integrated understanding of pre-Hispanic Andean coastal organization through a careful combination of archaeology and ethnohistory.

This study has three major sections: introductory and background material (Chapters 1–4), archaeological data from Lo Demás, the Chincha fishing settlement (Chapters 5–10), and summary and conclusions (Chapters 11–12).

CHAPTER 2

THE ECONOMIC ORGANIZATION OF CHINCHA: ETHNOHISTORIC DATA

This chapter discusses the ethnohistory of Chincha, located on the southcentral coast of Peru, and contrasts it with the documentary data for the Peruvian north coast.

The Ethnohistory of Chincha

Sources

Rostworowski (1970) provides the most complete review of the available documentary data on late pre-Hispanic Chincha (*see also* Menzel and Rowe, 1966). The valley and the polity it contained are often mentioned by the early chroniclers, but it is Cieza, in his *Crónica del Perú* (1984 [1550]) and *Señorío de los Incas* (1985 [1553]), who provides the most detailed information.

In addition to Cieza, the other primary sources of published information on late pre-Hispanic Chincha are two related documents concerned mainly with the nature of Inka governance and tributation: "Relaçión y declaraçión del modo que este valle de Chincha y sus comarcanos se governavan antes que oviese yngas y después q[ue] los vuo hasta q[ue] los cristianos entraron en esta tierra,"[1] by Castro and Ortega Morejón (Crespo, 1975), henceforth referred to as the "Relación"; and "Aviso de el modo que havía en el govierno de los indios en tiempo del inga y como se repartían las tierras y tributos"[2] (Rostworowski, 1970), henceforth referred to as the "Aviso." The "Relación" was written in 1558; although the "Aviso" has no date, Rostworowski (1970:140) uses internal evidence to place it between 1570 and 1575. Following Lohmann (1966) and Wedin (1966), Rostworowski (1970:138–140) argues that the similarities between the "Relación" of Castro and Ortega Morejón and the anonymous "Aviso" (as well as two other documents which do not directly concern Chincha) were based on as-yet undiscovered writings of Fray Domingo de Santo Tomás, a Dominican friar who founded the first monastery in Chincha (ca. 1542) as well as a monastery in the Chicama valley on the north coast of Peru. Rostworowski (1970:139–140) suggests that Cieza also drew on Santo Tomás for some of his information about Chincha. The differences between the documents indicate that "each author added his own information" (Rostworowski, 1970:140).

Several issues of interpretation concerning the "Relación" and the "Aviso" are directly involved in understanding late pre-Hispanic Chincha. First, which information refers to Chincha, and which refers to other valleys or to the Inka empire as a whole? Second, how much of the information concerning Chincha reflects conditions that originated under Inka rule and how much reflects the survival of local customs and traditions? The documents provide some internal clues to answer these questions, but a combination of ethnohistory and archaeology provides a fuller understanding of pre-Inka and Inka Chincha because of the greater time depth and material basis of the archaeological data.

Third, to what degree do the documents reflect conditions brought about by the Spanish conquest, considering that they were written 26 and 38 to 43 years after that event? The stated intent of both the "Relación" and the "Aviso" is to describe pre-Hispanic conditions; the full titles of both documents make this clear. The authors of the "Aviso" and the "Relación" do refer to postconquest conditions, but they do so quite explicitly, in order to make contrasts with the pre-Hispanic situation.[3] Furthermore, if Rostworowski (1970:138–140) is right (as seems likely) that both documents drew on information provided by Santo Tomás, then both are based on observations made within ten years of the conquest. Finally, Hernándo de Santillán (the author of one of the other documents which Lohmann [1966], Wedin [1966], and Rostworowski [1970] found to be derived in part from a common source) makes the following statement concerning the method of gathering information

> "The relation of these [facts] can only be given because they have been taken from old Indians by persons who know their language"[4] (Santillán, 1968 [1563–1564]:103).

A more likely problem than whether or not the documents *refer* to pre-Hispanic conditions is the *accuracy* with which they reflect the native Andean world. The information from native informants had to pass through the filter of translation and then be fit into a European conception of the world. Distortion could hardly be avoided. Furthermore, the Andean peoples had no system of writing; history was kept through oral tradition and with knotted strings called *quipos* or *quipus* (Santillán, 1968 [1563–1564]:103). Nor was the Andean region culturally homogeneous, despite the best efforts of the Inka idealogues (*see,* for instance, Silverblatt, 1988; also Netherly, 1977:292). The author of any document which synthesized conditions in the Andes—such as the "Relación" or the "Aviso"—had to make choices among the competing versions of history and custom. As Santillán (1968 [1563–1564]:103) admits in the preface to his account of the "origin, lineage, policy, and government of the Incas," "they are varied peoples and their accounts [are] in some things different."[5]

Returning to the first question, that of Chincha versus general information in the two documents, Rostworowski's (1970:137) cogent analysis of the "Aviso" is worth quoting at length:

> "To judge by the title, the anonymous author [of the "Aviso"] wished to write about the government and administration during the Inka reign, not in a local manner but rather in a general way. But despite his ambitious purpose, the writer, perhaps without realizing it and from the third paragraph, speaks of Chincha; and when he does so, he leaves the use of the verb in the past tense, and in the present tense says '. . . and now there are no more than 600' (tribute-payers). Then he returns to his impersonal narration dealing with the Inka empire in general, until folio 270 and its verso, when he abandons the monotonous tone to use the present tense and mentions 'the many vacant lands in Chincha.' From that point forward the data are now regional, as much in the information concerning the pre-Hispanic epoch as in that referring to the moment in which he wrote."

In the "Relación" (Crespo, 1975), Castro and Ortega Morejón usually signal the information referring to Chincha with the phrase "in this valley" ("en este valle"). They add an appropriate qualifier if the information applies as well to the neighboring valleys or to the coast as a whole (e.g., "en este valle y en todos estos llanos"). Unqualified statements probably refer to the Inka empire as a whole.

In the discussion of Chincha organization later in this chapter, I follow these guides to distinguishing between Chincha and general information in the "Aviso" and the "Relación." The general information may well apply to Chincha and—given the local source of data for the two documents—much of it probably derived from there. However, congruity cannot be assumed *a priori.*

The documents alone do not resolve the second question, concerning pre-Inka versus Inka traditions in the documents. Although the title of the Castro and Ortega Morejón's "Relación" (Crespo, 1975:93) speaks of "the way in which this valley of Chincha and its neighbors were governed before there were Incas and after they came," only the first two paragraphs directly discuss pre-Inka conditions (socio-political structure and foreign relations of the south coast valleys). The document then describes the Inka conquest of the south coast, the later history of Inka successions and conquests, and the customs and laws of the Inka. In discussing the inheritance of goods and offices, the "Relación" speaks of pre-Inka and Inka traditions of both coast and highlands, but it is unclear which information (if any) refers to pre-Inka custom (Crespo, 1975:100–101). The "Aviso" attributes essentially the same information to the Inka (Rostworowski, 1970:165). Only in the penultimate paragraph do Castro and Ortega Morejón (Crespo, 1975:103) again mention an explicitly non-Inka custom of the coastal peoples (*yungas*), who they say "did not worship the sun but rather the huacas [shrines or sacred objects]."[6]

The title of the "Aviso" refers solely to Inka times ("el tiempo del inga"). Only one phrase in the document mentions explicitly pre-Inka conditions: in Chincha, "there was a single great lord whom all of the people respected and obeyed, *this was before Thupa 'Inka Yupanki*"[7] (Rostworowski, 1970:170, emphasis added).

Cieza, "the most anthropological of chroniclers" (Murra, 1980:187), differentiates clearly between pre-Inka and Inka conditions. He also warns that

> "As the Inka became [the Chincha's] lords, [the Chincha] took from them many customs, and used their clothing, imitating them in other things that [the Inka] ordered, as the sole lords that they were"[8] (Cieza 1984 [1550]:221, Cap. LXXVIIII).

Menzel and Rowe (1966:68) place the first contact between the Chincha and the Inka in the 1440s, whereas the final annexation of the valley under Thupa Yupanki took place around 1476. Thus, at the time of the Spanish conquest in 1532, Chincha had felt Inka influence for nearly a century, and had been under direct Cuzco control for over 50 years. Murra (1980:162) notes that the Inka rulers rewrote their own history to further the cause of victors in the struggles of succession, while Silverblatt (1988) has shown that the Inka attempted to legitimize their rule by altering the very history of the peoples they conquered. Although the Inka were not fully successful in the Empire at large (many of their subject peoples allied themselves with the Spanish invaders), such attempts at manipulating the past call into question that information in the two documents which explicitly describes pre-Inka conditions. The statements concerning Chincha during Inka rule are even less reliable as a guide to pre-Inka conditions. This is not to deny that local traditions and biases influenced perceptions of pre-Inka and Inka history and customs in Chincha and elsewhere; variation abounded, but original conditions and events can still be masked. In her analysis of the "Aviso" and elsewhere, Rostworowski (1970:144, 1977 *inter alia*) considers that the economic organization of Chincha as seen in the document reflects a pre-Inka pattern. This may well be true. However, for reasons discussed above, caution must be exercised in making such an assumption from the documentary evidence alone; ultimately, the question must be answered through archaeological research.

Late Pre-Hispanic Chincha

In the following section, I synthesize the information from Cieza, the "Relación," and the "Aviso" concerning late pre-Hispanic Chincha; the reader should bear in mind the caveats discussed in the preceding section. Although in many aspects this synthesis resembles those of Rostworowski (1970), in her commentary on the "Aviso," and Menzel and Rowe (1966), I have compiled the following version by returning to the original sources. Doing so has allowed me to focus more attention on areas of particular interest to this study; furthermore, I do not always agree fully with the earlier interpretations.

According to the "Relación" (Crespo, 1975:93), before the Inka conquest of the south coast, each *ayllu* (social unit) had its lord and its fields; the "Aviso" (Rostworowski, 1970:170) tells us that in Chincha, all were subject to a paramount lord. The coastal peoples worshipped *huacas* instead of the Inka sun god ("Relacion," Crespo, 1975:103). According to Cieza (1984 [1550]:219, Cap. LXXVIIII), the sacred place of Chincha was called "Chincha y Camay" (Chinchaycamac). Presumably, Chinchaycamac was a branch oracle ("son") of the great central coast shrine of Pachacamac; Santillán (1968 [1563–1564]:111) wrote that one of Pachacamac's "sons" was located in Chincha during Inka times (*see* Menzel and Rowe, 1966:68; Patterson, 1985:164, 167–168; Rostworowski, 1970:142). Menzel and Rowe (1966:68) believe that under the Inka, "Chincha . . . was not only subject to the Inca government but also to the oracle of Pachacamac." Patterson (1985:164) suggests that the Chinchaycamac branch oracle was established by the Pachacamac priests before the Inka conquest of the valley, in part to gain information on Chincha which the priests passed on to their Inka allies/lords. A pre-Inka origin for the *huaca* is consistent with Cieza's (1984 [1550]:220, Cap. LXXVIIII) statement that under the Inka, "the natives of Chincha did not stop worshipping also at their old temple of Chinchaycamac."[9] In any case, the presence of Late Horizon, Pachacamac–Inka and related pottery in Chincha sites (Uhle's sites and Lo Demás) demonstrates some real link between the two areas during the Inka rule of the coast (Menzel, 1966:112–113; Menzel and Rowe, 1966:68–69; Patterson, 1985:167–168).

Castro and Ortega Morejón ("Relación," Crespo, 1975:93) indicate that the south coast valleys lived in a state of constant warfare before the arrival of the Inka; Cieza (1984 [1550]:219, Cap. LXXVIIII) records an origin myth in which the late pre-Hispanic inhabitants of Chincha had conquered and exterminated an earlier race of midgets. The same account states that the Chincha carried out successful raids in the south highlands at the same time as the Inka were founding Cuzco. Accounts of pre-Inka endemic warfare such as those cited for Chincha may well be exaggerated in the chronicles; Inka informants often used this tactic to support the notion of the Inka as the civilizers of the Andes. However, recent archaeological research in different areas of the Andes has found an increased evidence for warfare (principally fortification) in the Late Intermediate Period, immediately preceding Inka conquest (*see* review in Parsons and Hastings, 1988).

According to Cieza (1984 [1550]:219–220, Cap. LXXIIII, 1985 [1553]:172, Cap. LX), the first contact with the Inka was an expedition sent by the Inka ruler Pachakuti Inka Yupanki under the command of Qhapak Yupanki. Dated by Menzel and Rowe (1966:68) to the 1440s, this expedition failed to subjugate Chincha; however, the peaceful incorporation of Chincha into the Inka empire was later carried out under Pachakuti's son Thupa Yupanki (Cieza, 1984 [1550]:220, Cap. LXXVIIII, 1985 [1553]:173, Cap. LX). Menzel and Rowe (1966:68) date this event to around 1476.

Castro and Ortega Morejón's version of the Inka conquest of Chincha ("Relación," Crespo, 1975:93–94; *see also* Rostworowski, 1988*a*:100–103) differs in that Qhapaq Yupanki successfully and peacefully incorporated Chincha and neighboring valleys into the empire; Thupa Yupanki consolidated Inka control of the valleys. As detailed in the "Relación," this process consisted of reordering the political structure into a decimal, Cuzco model with the Inka now holding the highest position in the hierarchy, imposing the Inka system of justice, and rechanneling tribute (in land, labor, and products) into the Inka state network. Wayna Qhapaq, Thupa Yupanki's son and the next Inka ruler, also imposed new levies in land and labor on his subjects, though the "Relación" does not refer specifically to Chincha at this point.

Cieza (1984 [1550]:220, Cap. LXXVIIII) records that the Inka built "large and sumptuous lodgings for the kings; and many storehouses . . . [and] a temple of the sun" in Chincha.[10] The temple was staffed with priests and virgins, and an Inka administrator (*mayordomo*) was placed over the valley. Nevertheless, "the Inka did not take dominion away from the lords and chiefs"[11] (Cieza, 1984 [1550]: 220, Cap. LXXVIIII), although like all vassals of the empire they were subject to Inka law. The Chincha lords were required to spend several months each year at court in Cuzco. The Inka sent *mitimaes* or *mitmaq*[12] to Chincha (Cieza, 1984 [1550]:220, Cap. LXXVIIII) and took people from Chincha for service elsewhere as *mitimaes.* During the early years of the Colonial Period, there were still *mitimaes* from Chincha in the neighboring valley of Cañete (Rostworowski, 1978–1980:166), and Chincha silversmiths were residing somewhere out of the valley, possibly in the Inka capital at Cuzco (Rostworowski, 1977:234). The "Relación" (Crespo, 1975: 96) also talks of *yanaconas* and *mamaconas*[13] who were placed in the service of the Inka or the sun, but Chincha is not specified in this section. However, the "Relación" (Crespo, 1975:99) does mention "an Indian woman in this valley of Chincha who was designated for the Inka"[14] only a few years before the Spanish conquest. Presumably, this woman was an *aclla* (chosen woman), perhaps one of the virgins who Cieza says were placed in the temple of the sun by the Inka. We cannot know if the *aclla* were from Chincha or from somewhere else.

Some fifty years after Thupa Yupanki's consolidation of the south coast, Chincha fell into Spanish hands along with the rest of the Andean world. By all accounts, Chincha at the time of the Spanish conquest was a marvelous place, famed throughout the Inka empire as a rich and powerful kingdom. Cieza (1984 [1550]:218, Cap. LXXIII) writes of the

> "beautiful and large valley of Chincha, as famed in all of Peru as it was feared in earlier times by most of the natives . . . when the Marqués don Francisco Pizarro with his thirteen companions discovered the coast of this kingdom [the Inka empire], everywhere they said that he should go to Chincha, which was the largest and best of all."[15]

Concerning Chincha itself, Cieza (1984 [1550]:220, Cap. LXXIII) records that "this valley is one of the largest of all Peru: and it is a beautiful thing to see its groves and canals, and how many fruits there are throughout it."[16] When the Inka ruler Thupa Yupanki arrived in Chincha after its people capitulated to him, "on seeing it so large and beautiful, he became very happy" (Cieza, 1985 [1553]:173, Cap. LX).[17]

As Menzel and Rowe (1966:68) point out,

> "Chincha had a notable reputation for wealth in precious metals, especially silver. The members of Pizarro's expedition picked up a report, recorded by Jérez [1862 {1534}:335], that the richest mines of precious metals were at Quito and Chincha."

The record of early Spanish looting in the valley supports Chincha's reputation for wealth. The "Aviso" (Rostworowski, 1970:171–172) states that

> "by order of Hernando Pizarro, [Thomas de Hontiveras and Diego de Mesa] took from the tombs of the dead Indians that were next to the first monastery that Father Fray Domingo de Santo Tomás . . . founded in said valley . . . one hundred thousand marks of silver in large vessels and small ones and other . . . [objects] all in gold and silver. . . . And after that much gold and silver has been taken from that valley and there is much more to be taken. . . ."[18]

Menzel and Rowe (1966:footnote 29) list other early accounts of the looting of Chincha. They also note (Menzel and Rowe, 1966:68) that as late as 1901, silver was still common even in poor graves excavated in Chincha by Uhle (1924; Kroeber and Strong, 1924). Rostworowski (1970:143) points out that the "Aviso" mentions cemetery guards, "which reveals the fear of the lords, since those [pre-Hispanic] times, of the sacriligious robbery of their tombs." (However, the citation concerning guards comes from the part of the document which refers to the Inka empire at large, and not specifically to Chincha.) It is hardly surprising, then, that Chincha was so famous among the Spaniards; precious metals were of paramount importance to the European invaders. For this reason, the early chroniclers may well have overstated the importance of Chincha in the Andean world.

None of the explicitly pre-Inka information discusses the Chincha economy, beyond Cieza's (1984 [1550]:219, Cap. LXXVIIII) general statement that before the expansion of the empire under Pachakuti, "the kingdom of [the Chincha] was always secure and prosperous."[19] Concerning the economic (and related social and political) organization of Chincha under the Inka, the "Aviso" provides the most information. At the time of the Spanish conquest "there were in the valley of Chincha and its jurisdiction thirty thousand tribute-paying men"[20] ("Aviso," Rostworowski, 1970:170). Lizárraga (1946 [ca. 1605]:90, Cap. XLVII) also mentions 30,000 tribute-payers in his chapter on Chincha, which is a close copy of the "Aviso" (Rostworowski, 1970: 137). In the "Aviso," however, the 30,000 were divided into 12,000 farmers (*labradores*), 10,000 fishermen (*pescadores*), and 6,000 merchants (*mercaderes*) ("Aviso," Rostworowski, 1970:170–171); the missing 2,000 tribute-payers are not mentioned. Lizárraga (1946 [ca. 1605]:90, Cap. XLVII) solved this discrepancy by dividing the population into three groups (farmers, fishermen, and merchants) of 10,000 each, but this version is too neat to be likely. Lizárraga also includes *plateros* (silversmiths) among the *labradores,* whereas the "Aviso" restricts *labradores* to farmers. Each of the groups was apparently specialized.

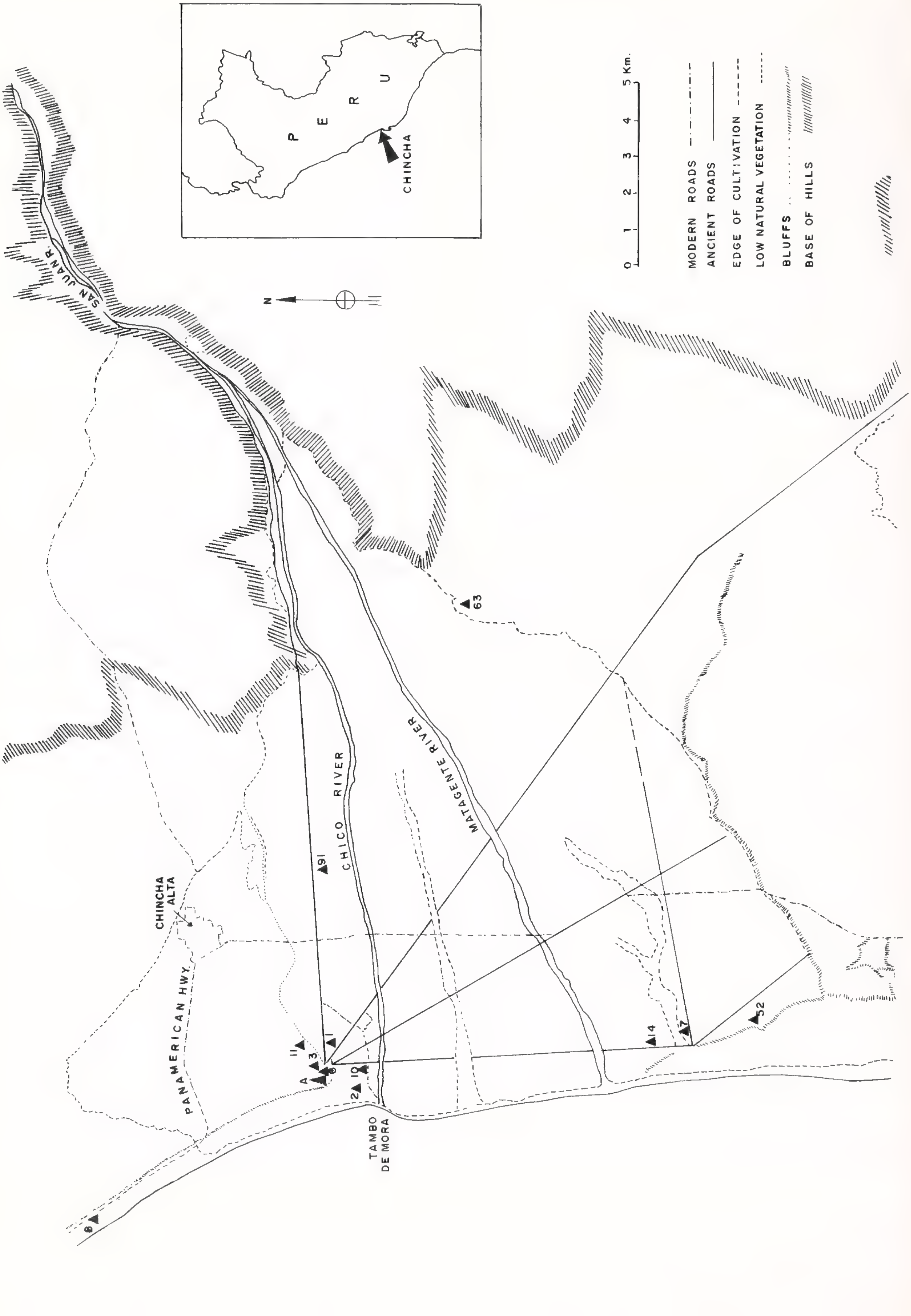
The "Aviso" emphasizes that the 30,000 Chincha tribute-payers were divided into groups of 1,000, each under its own lord; there were "thirty caçiques [lords or chiefs] of said [tribute-payers], each one of whom had one thousand Indians in his charge, and all these thirty were lords"[21] ("Aviso," Rostworowski, 1970:170). The decimal administration system was Inka in origin (Julien, 1988; Murra, 1980: 112); both the "Aviso" and the "Relación" discuss this system in the sections on the Inka empire at large, and the "Relación" (Crespo, 1975:94) quite specifically states that Thupa Yupanki "in imitation of Cuzco divided the Indians and put lords in such a manner that there was a curaca [lord, chief] of a thousand Indians,"[22] with chiefs of 100 Indians under him, and heads of ten below them. It is unclear how strictly the decimal system was followed throughout the empire or how it was implemented in each province (Julien, 1988), but information in the Chincha documents indicates that the lords of the valley were at least nominally organized on this principle: groups of 1,000 are mentioned, the different specialists are counted in multiples of 1,000, and the number of *caçiques* is equal to the total population of Chincha divided by ten (*see above*).

Recalling Cieza's (1984 [1550]:220, Cap. LXXIIII) statement that the Inka left the indigenous lords in power (though subject to Inka rule and law), it seems likely that many of the thirty *caçiques* and their subordinate chiefs were natives of Chincha; however, some may have been lords of the *mitimaes* whom the Inka brought to Chincha. Finally, there was a lord over the entire valley (in addition to the Inka administrator); he is the man who accompanied Atawalpa in Cajamarca in 1532, during the initial encounter with Francisco Pizarro (Pizarro, 1965 [1571]:232).

The documentary data suggest, but do not explicitly confirm for Chincha, that the population of the valley under the Inka was also organized according to a principle of duality. The "Relación" of Castro and Ortega Morejón states that Thupa Yupanki ordered "that in all the valleys there were to be two *parcialidades* [social units] one that was to be called *hanan* and the other *lorin*"[23] (Crespo, 1975: 94). The "Aviso" (Rostworowski, 1970:170) mentions "Lurinchincha," which implies the existence of "hananchincha" and thus some sort of dual division along the lines indicated by the "Relación."[24] One of the two largest Late Horizon site complexes in the Chincha valley (the San Pedro complex, PV 57–7) lies on the southern margin of the valley near the ex-hacienda called Lurinchincha; the other complex is the apparent Chincha capital and Inka administrative center of La Centinela, on the north side of the valley (*see* Chapters 4 and 5 and Fig. 1). The two sites were connected by a straight road which Wallace (1972:3) identified from aerial photographs. San Pedro and La Centinela may represent the nuclei of the two *parcialidades* in late pre-Hispanic Chincha (Wallace, 1991:258).

As Rostworowski (1970) has argued, the "Aviso" clearly indicates that the farmers (*labradores*) and fishermen of Chincha were specialists. The farmers "understood only the planting of maize and other seeds and roots with which they sustain and maintain themselves" ("Aviso," Rostworowski, 1970: 170).[25] The "Relación" of Castro and Ortega Morejón (Crespo, 1975:101–102) discusses tribute paid by the inhabitants of Chincha and neighboring valleys in the form of labor in fields assigned to the reigning Inka, previous Inkas, the sun, and the *huacas.* The fruit of this labor "was put in storehouses from which it was taken to Cuzco and to Jauja and to Pachacamac or wherever [the Inka] ordered it"[26] ("Relación," Crespo, 1975:101). This form of tribute must have been paid by those whom the "Aviso" calls farmers (*labradores*). As we shall see below, the fishermen only fished. The document does not specify the obligations of the merchants in terms of agricultural or other labor beyond their special trade.

Concerning the fishermen, the "Aviso" provides more detailed information:


PERU
CHINCHA
0 1 2 3 4 5 Km.
MODERN ROADS
ANCIENT ROADS
EDGE OF CULTIVATION
LOW NATURAL VEGETATION
BLUFFS
BASE OF HILLS
N
SAN JUAN R.
CHICO RIVER
MATAGENTE RIVER
CHINCHA ALTA
PANAMERICAN HWY.
TAMBO DE MORA
63
16
11
1
3
A
8
10
2
14
7
52
8

> "There were settled along the shore ten thousand fishermen, who each day or the better part of the week entered the sea, each with his raft and nets and they left and entered their indicated and known ports, without competing one with the other, because they had in this as in the rest, great order and concert and love and fear of the Inka and their caçiques [lords] and these [fishermen] were settled from two leagues before arriving at Chincha to another part of Lurinchincha [sic], that has from one part to the other five leagues; and the settlement of these people seemed like a beautiful and long street full of men and women, boys and girls, all content and happy because when they were not entering the sea [to fish], all their care was to drink and dance, and so on"[27] ("Aviso," Rostworowski, 1970:170–171).

This citation makes several assertions about the fishermen: 1) they worked only at fishing, while their life on land was happy and carefree; 2) they lived in a separate settlement along the shore; 3) they had their own lords (*caçiques*), presumably lords of 1,000 tribute-payers and lower level chiefs; and 4) the organization and order of their fishing activities were maintained under the authority of the fishing lords and the Inka. The first point makes the specialist status of the fishermen clear; if all they did was fish, dance, and drink, then they could not have worked in the fields or on other local or state corvée labor projects. The second point, residential isolation, is a key factor in enabling archaeological identification of this segment of the Chincha population (*see* Chapter 5). The fishermen are the only group of Chincha specialists whose settlement is described and located in the documents. Concerning the third point, the "Aviso" numbers the specialist groups in multiples of 1,000 (*see above*); probably the lords of 1,000 tribute-payers were counted instead of individuals. This, in turn, implies that the 10,000 fishermen had ten major divisions and that these divisions were organized politically as well as economically. Given that the decimal system was an Inka imposition, it is clear that the Inka had restructured the fishing groups—at least nominally—by the time of the Spanish conquest; the same conclusion applies to the farmers and merchants.

The third Chincha economic group mentioned by the "Aviso" is the merchants. Rostworowski (1970: 135) considers the information on this group as the most original and important part of the document, and she presents a detailed analysis of the evidence for merchants in the Andean world (Rostworowski, 1970:145–157). Limiting ourselves to what the "Aviso" says, we learn that the 6,000 merchants of Chincha traded south to Cuzco by land and north to Puerto Viejo and Quito in Ecuador, presumably by sea to Puerto Viejo and then inland to Quito (Rostworowski, 1970:171). The land trade to the south most likely would have involved llamas for transport; Cieza (1984 [1550]:220, Cap. LXXVIIII) refers to the many camelids in Chincha before the civil wars among the Spanish Conquistadores. The large number of merchants listed in the "Aviso" suggests to Rostworowski (1970:155–156) that inland trade involved porters as well as llamas.

The maritime trade presumably used balsa trading rafts similar to that seen by Bartolome Ruyz off northern Ecuador during Pizarro's second expedition, in 1525 (Samano-Xérez, 1967 [1527–1528]: 65–66). Recounting the events in Cajamarca in 1532 when Atawalpa (the Inka ruler) met and was captured by the Spaniards, Pedro Pizarro (1965 [1571]: 232) wrote that Atawalpa told him of his great friend the lord of Chincha, who had "100,000 balsas [trading rafts] on the sea." Although necessarily an exaggeration, this association of the lord of Chincha with balsas and with the Inka ruler demonstrates that Chincha was involved in significant maritime activities under the Inka.

The "Aviso" lists some of the goods traded by the Chincha merchants; from Ecuador they brought "many beads of gold and many rich emeralds, which they sold to the caçiques of Ica"[28] ("Aviso," Rostworowski, 1970:171). Rostworowski (1970:152) believes that another, perhaps the major, product brought from the north was *mullu* or *Spondylus* shell. This red and white bivalve is indigenous to the warm waters of Ecuador, and it played a very important role in agricultural rituals throughout the Andes (*see* Chapter 9, section on mollusks). However, the "Aviso" does not actually mention *mullu* at any

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Fig. 1.—Map of the Chincha valley, Peru, showing principal geographic features and archaeological sites mentioned in the text. Adapted from Wallace (1971:endpiece). Modern towns and geographic features are named on the map. Numbers are PV 57–site codes from Wallace's (1971) survey report; letters are sites not listed by Wallace. Site codes: A = Lo Demás; B = Jahuay; 1 = La Centinela; 2 = Huaca de Tambo de Mora; 3 = El Cumbe; 6 = Uhle's Cemetery B; 7 = San Pedro complex; 10 = Huaca del Alvarado (Uhle's Site D); 11 = Uhle's Cemetery E; 14 = Ranchería; 52 = Pozuelo; 63 = unnamed; 91 = Huacarones.

point. The document is silent as well concerning the goods acquired in the south.

The "Aviso" offers the surprising news that of all the Inka empire, only the Chincha merchants used a form of money; "among themselves they bought and sold with copper what they had to eat and to clothe [themselves]"[29] ("Aviso," Rostworowski, 1970:171). Each piece of copper had a fixed value and gold had a fixed exchange rate with silver.

What the "Aviso" does not tell us is that the merchants were pre-Inka in origin. Rostworowski (1970:144, 1988*a*:103)[30] believes this to be the case; her logic is twofold. First, she argues that Chincha capitulated peacefully to the Inka because they wanted to avoid disruption of their profitable trading activities. Second, believing that *Spondylus* was the principal trade item acquired in the north, she argues that the Inka would have allowed the Chincha merchants to continue their activities in order to assure adequate supplies of the sacred *mullu* (the northern habitat of this shell was incorporated into the Inka empire only very late in its history). Thus, Rostworowski (1970:144) sees the Chincha merchants under the Inka as "a last trace of former times," a sort of necessary evil in an imperial economy based mainly on state-administered redistribution.

Although Rostworowski may be correct concerning the pre-Inka *origins* of the Chincha merchants, several features of the documentary and archaeological records suggest that Chincha's long-distance trading expanded greatly under Inka rule, and that the possibility of *increased* (as opposed simply to continued) trading activity was one of the inducements to capitulate to Thupa Yupanki. Of the foreign (non-Chincha) pottery identified by Menzel (1966) from the Uhle Chincha collections (*see* Chapter 4), virtually all pieces come from contexts postdating the Inka conquest of the valley. The "Relación" of Castro and Ortega Morejón ("Relación," Crespo, 1975:93) says that before the Inka, the south coast polities lived in a state of constant warfare, and that the Indians did not

> "pass from one part to another nor know—unless by hearsay—that there were more people because if they passed if it was not in time of peace and treaties they killed one another."[31]

Even with occasional moments of peace, such a situation would have been far less conducive to successful trading than would a privileged status under the *pax incaica.*

Also problematic for assigning Chincha a major role in pre-Inka long-distance trade is the presence of the powerful Chimu kingdom on the north coast, squarely on the path to Ecuador. If *Spondylus* was the major item acquired in the north by the merchants, why is it so common in the late pre-Hispanic sites of the north coast—Chimu territory—and so rare in Chincha, where its known archaeological occurrences are exclusively Inka in date?[32] Shimada (1991:LIV) suggests that

> "the emergent Chimú state probably came to be the principal North Coast sponsor of maritime trade . . . while the specialized Chincha traders described in a colonial document . . . managed the actual operation of the trade, including navigation."

This hypothesis accepts the pre-Inka existence of the Chincha traders as given, and fails to account for the pre-Inka absence of northern items in Chincha. Also, Shimada does not explain why the Chimu would rely on traders from another region when it surely had a well-developed seafaring capacity; cargo-carrying rafts appear in North Coast art as early as Moche V, ca. A.D. 600–750 (McClelland, 1990), and nothing in the iconography suggests that they are foreign vessels.

Unlike Chincha, Chimu resisted Inka rule and as a result was severely reduced in power and extent after its defeat (*see* Netherly, 1977:313–314 ff., 1988*a*:115–122). According to Cieza (1985 [1553]: 169–173, Caps. LIX–LX), Thupa Yupanki conquered Chimu not long before he turned to the south coast and incorporated Chincha into the empire. Referring to Chincha's peaceful capitulation to the Inka, Netherly (1988*a*:111) remarks that "it would be of great interest to know the nature of the deal that was made." As part of the deliberate destructuring of the Chimu kingdom, might not Thupa Yupanki have offered the lords of Chincha trading rights which were formerly the prerogative of Chimu? Such an offer would have made peaceful capitulation an attractive prospect (Sandweiss, ms.); Hyslop (1984: 102) also suggests that "the power and prestige of Chincha actually increased during the period of Inka alliance/domination."

In addition to the farmers, fishermen, and merchants, the "Aviso" lists a number of artisans and others who carried out specialized work, including servants in *tambos* (Inka state installations), bridge-keepers, *chasquis* (messengers), *huaca* and cemetery guards, herders, carpenters, sling-makers, sling-stone gatherers, makers of fine clothing, metalsmiths, and miners ("Aviso," Rostworowski, 1970:167–169). All of these *oficiales* (specialists) are mentioned in the part of the document which refers to the Inka empire in general. The makers of fine clothing are specified as *serranos* (highlanders). Both the highlands and the coast had herders. Miners were to be recruited from the natives of lands which had gold or silver mines. For the other *oficiales,* the "Aviso" provides no clue as to their distribution within the empire. However, Falcón's 1571 list of "offices and things in which they served the Inka,"[33] transcribed by Rostworowski (1977:248–250), includes the following occupations of the coastal Indians also cited in the "Aviso": miners, makers of fine cloth, fishermen, potters, carpenters, and farmers. The section on highland occupations lists all of these coastal *oficiales* except the fishermen. Falcón also lists a wide variety of other coastal and highland *oficiales.*

In general, the Inka ordered "those who were *oficiales* to pay tribute in the thing of their office and no other"[34] ("Aviso," Rostworowski, 1970:169). The "Aviso" (Rostworowski, 1970:168–169) provides specific examples of *oficiales* tribute obligations vis-à-vis the Inka state.

The document granting the Indians of Chincha in *encomienda*[35] to Hernando Pizarro (Rostworowski, 1977:234) mentions Chincha silversmiths living outside of the valley as *mitimaes*; as Rostworowski (1970:159) notes, Lizárraga (1946 [ca. 1605]:90, Cap. XLVII) wrote early in the 17th century that "among these laborers [of Chincha] there were some artisans [who were] good silversmiths and today there are still some."[36] I know of no specific *documentary* evidence for other categories of artisans in Chincha.

THE CHINCHA ECONOMY: ETHNOHISTORIC MODEL ONE

According to sources referring specifically to Chincha under Inka rule, the population of Chincha was composed of three major groups: the farmers, the fishermen, and the merchants. The farmers and the fishermen were definitely specialized, working at and paying tribute only through the activities of their specialty; presumably, the merchants were similarly specialized. The fishermen (at least) had their own settlement, separate from the rest of the population. There may have been specialists (*oficiales,* e.g., artisans, herders) other than fishermen, farmers, and merchants in Chincha, but we can be sure only of the silversmiths. Each of the specialized groups was organized according to the Inka decimal system into units of 1,000 tribute-payers, with a hierarchy of lords and headmen leading nested divisions of 1,000, 100, and 10 tribute-payers. The valley as a whole was subject to the lord of Chincha as well as to the Inka administrator. The people of Chincha bought and sold food and clothing with copper pieces. Also present in the valley were *mitimaes* colonists from unspecified areas and in unknown numbers, and *aclla* living in the temple of the sun and working for the state. In addition to the contacts with other areas of the empire through participation in the activities of the state (e.g., sending tribute to Cuzco and elsewhere), the Chincha had two other modes of long-distance contact: their spetial connection with the central coast shrine of Pachacamac, and the trading expeditions of the merchants north to Ecuador and south to the highlands around Cuzco.

This rather simple picture raises many unanswered questions. How were the farmers, fishermen, and merchants integrated into a single polity? Was copper money really in use, or were there other mechanisms of exchange among different segments of the Chincha population? Which of the coastal occupations other than farmers, fishers, merchants, and silversmiths were present in Chincha? The documents do not tell us how the Chincha artisans were organized, nor how they interacted with the other groups. How did they fit into the decimal structure? Are they the missing 2,000 tribute-payers in the "Aviso's" account of the 30,000 Chincha *tributarios*?[37] Even if the general sections of the "Aviso" are taken to apply to Chincha, we learn only that *oficiales* paid tribute in their specialized product or service; some worked fields for their own support, while others apparently did not. We do not know if the Inka administrators had *yana* (male retainers) working for them, nor if they gave *aclla* and *yana* to the local lords (a common practice according to the "Relación" [Crespo, 1975] and other sources (*see* Murra, 1980:Chapter VIII). And, of course, to what degree does the ethnohistoric "picture" of Chincha reflect pre-Inka conditions? Some of these questions will remain unanswered, but the following sections and chapters shed light on many of them.

THE NORTH COAST

The picture of the late pre-Hispanic Chincha economy reconstructed above from purely local sources is rather simple; an examination of the contemporary north coast record offers a more complex picture, but one which must be applied even more tentatively to Chincha prior to archaeological testing.

Sources

Known ethnohistoric sources for the north coast of Peru are more abundant and varied than the south coast documents. In addition to the chroniclers, there are a number of *visitas* (inspections) and other legal and administrative documents which provide a wealth of information on the area. In this section, I rely on several recent, detailed studies of north coast ethnohistory (Hart, 1983; Netherly, 1977, 1984; Rabinowitz, 1983; Ramirez-Horton, 1982; Rostworowski, 1977, 1981), in part because so many of the data cited by these authors are otherwise unavailable.

Many of the same caveats concerning Inka and pre-Inka information discussed above in the case of Chincha also apply to the north coast data (Hart, 1983:126; Netherly, 1977:292). The information in this section can be taken as reflecting conditions under Inka rule. The nature of the pre-Inka (Chimu) structure is left open for the moment; I will return to this issue in Chapter 12.

The Late Pre-Hispanic North Coast

The economic organization of the north coast of Peru in the period just preceding the Spanish conquest was based on occupationally-defined groups, as at Chincha; more such groups are named. The documentary data for the north coast offer more explicit definitions of the structure and interrelations of these specialists.

Netherly (1977, 1984:229–234) has shown that duality was the dominant organizing principle of north coast *parcialidades* (basic social and economic units subject to a local level lord). This duality operated at several hierarchical levels. "At the primary or lowest level the *parcialidades* were grouped by economic activity," with the most common being the farmers, followed in number by the fishermen and then the other specialists. However, "the presence of both fishing and farming groups was considered to be necessary and an integral component of higher levels of organization" (Netherly, 1984: 231). The relationship of paired groups at each hierarchical level was asymmetrical, with the lord of one half subordinate to the lord of the other half. At the highest level within each pre-Hispanic polity or Spanish *repartimiento* (Spanish administrative units roughly parallelling preconquest polities within the Inka empire), there was a paramount lord or *caçique principal* (Netherly, 1984). Hart (1983:253–254) writes that "in general, specialist groups seem to have been subordinate to a *caçique principal* whose closest affiliation (i.e., his particular *parcialidad*) was with agriculturists."

Ramirez-Horton (1982:125, Table 1) lists 24 categories of artisans/specialists known from one or more 16th century sources for six north coast polities in the area of present-day Pacasmayo and Lambayeque. Among these categories are the fishermen and merchants also named in the "Aviso" for Chincha (farmers are not listed here, as they were considered to be generalists). Fishermen are the only specialists known from all six polities, and they generally appear in the earliest source for each area. Of the categories of specialists named in the general section of the "Aviso," the carpenters, potters, herders, metalworkers (silversmiths), shoemakers, and various categories of clothing makers are also listed for the north coast polities; in other words, all of those specialists from the "Aviso" who might be considered as artisans or craftsmen.

Hart (1983) offers two useful criteria for classifying specialists on the north coast. The first criterion is whether or not the specialists were associated directly with the lords:

> "The first category is those specialists who were directly associated with a *caçique.* They either acted as agents of the *caçique* or were important to the enhancement of his status. Included in this status are the cooks and hammock bearers, at least some of the chicha [corn beer] makers, silversmiths, merchants (Ramirez-Horton, 1982), textile workers, and other producers of luxury goods. The second type of specialist was of importance to the economic life of the *repartimiento* or valley, but apparently was not directly associated with the *caçiques* . . . Such specialists included fishermen, saltmakers, carpenters, spindle makers, potters, basketmakers, shoemakers, and deer hunters" (Hart, 1983:255).

The specialists of the second category often had their own settlements, usually located near the specialized resource which they exploited (Netherly, 1977: Chapter VI, *passim*). Fishermen, in particular, lived near the shore, apart from other groups. Ramirez-Horton (1978:90–92; *see also* Rostworowski, 1981: 116–117) cites a 1572 document for the Saña valley which discusses several settlements, including Cherrepe, a village of fishermen located near the sea.

The specialists' lords sometimes held high rank in their polity. For instance, Hart (1983:240) refers to a *caçique principal* of the fishermen of Malabrigo, in the Chicama valley, who was probably the number two lord in the local hierarchy. Given such high rank, lords of Hart's second category of specialists (e.g., fishermen) probably had attached specialists of the first category (e.g., cooks, silversmiths).

Hart's (1983) second criterion for classifying north coast specialists is whether or not they farmed in addition to carrying out their specialized activity:

> "Included in the group who cultivated no lands were cloth painters, potters, fishermen, merchants, *chicha* makers, and saltmakers. Cooks, mat makers, and deer hunters, however, also worked lands in addition to their respective specialized activities. . . . Whether or not other specialists did or did not have lands cannot be demonstrated from the available data" (Hart, 1983:268).

This division is essentially that between full-time and part-time specialists.

There is some overlap in the categories of specialists which Hart could classify according to the two sets of criteria (cooks, fishermen, saltmakers, potters, and *chicha* makers). Those who did not work land were most often in the group of those specialists not directly associated with the *caçiques*; thus, the fishermen were independent specialists who did not farm. The specialists who also cultivated lands included one of the categories (cooks) directly associated with the *caçiques.*

Members of all households carried out some specialist activities on a domestic level. Certainly, every domestic unit included one or more persons who cooked. The women of the north coast agricultural households engaged in cloth production (Netherly, 1977:249), though it is not clear if the women in fishing households also wove. Some of the 16th century petitions by fishermen talk of trading fish for cotton, among other necessities (e.g., Netherly, 1977: 241). Was this cotton only for nets, or also for cloth?

The specialist status of the north coast fishermen is particularly well attested in the ethnohistoric record. Hart (1983:272–273, 276–277), Netherly (1977: 237–241), Ramirez-Horton (1982:128–129), and Rostworowski (1977:222) all cite and cross-cite 16th century petitions from fishermen stating that the fishermen had no (or few) fields, that they paid tribute in fish, and that they earned their living by fishing and trading fish for their other necessities. In these documents, the fishermen generally petition to be freed from agricultural tribute and/or for permission to move about in order to trade their fish with neighboring villages and *repartimientos.* In one court case from 1595 (Hart, 1983:276–277), fishermen from the town of Moche in the north coast Moche valley testified that they went to Simbal in the middle valley to exchange fish and other items.

The petitions were most often presented by men who identified themselves as lords (*principales*) of fishing groups. Like the Chincha fishermen in the "Aviso," the north coast fishermen had, in the words of a fishing *principal* in 1566, "known and private places" where each group fished[38] (Rostworowski, 1977:225). The north coast fishermen apparently had their own dialect, referred to in the early documents as "pescadora" (Rabinowitz, 1983; *see also* Netherly, 1977:90–91; Rostworowski, 1981:95–100).

The evidence for merchants on the north coast has been discussed in detail by Netherly (1977:252–270), Ramirez-Horton (1982), and Rostworowski (1977:257–260). Virtually all of the data concern what Netherly (1977:Chapter VI, *passim*) calls intraregional exchange and are limited to the Lambayeque area discussed by Ramirez-Horton (1982; Netherly, 1977:254). In addition to the exchange of specialized produce between the various specialist groups, such as the fishermen discussed above, there were also *parcialidades* specialized in exchange itself; these groups did not plant fields (Netherly, 1977: 255–258).

Evidence for long-distance exchange such as that which the "Aviso" describes for the merchants of Chincha is tenuous at best, and concerns only coast–highland exchange (Netherly, 1977:258–270).

Most of the information on the merchants comes from the mid-16th century, and Ramirez-Horton (1982) has questioned the exact nature of these groups during pre-Hispanic times. She suggests that

> "what the Spanish early identified as merchants might have been in reality *mitayos* (temporary drafted laborers) or porters, retainers of the lords, carrying tribute and supplies between the various settlements within a lord's jurisdiction for distribution or storage" (Ramirez-Horton, 1982:132).

If this was the case, then the north coast merchants of the Late Horizon were agents of the lords or the state, and not independent traders. If the long-distance merchants were retainers of the highest lords, that would account for their scarcity at the time of the Spanish conquest; it was the Chimu state apparatus which the Inka dismantled most thoroughly. This scenario would provide a rationale for the replacement of Chimu traders with Chincha merchants by the Inka, as suggested above.

The nature of tribute provides a final point of interest concerning north coast organization. In their petitions to the Spanish officials, the specialists tended to claim that they paid tribute in their specialized produce, and not in agricultural or other general labor for the lords or the state. This is particularly true of the fishermen (*see* references cited above). The farming segment of the population provided most of the tribute in agricultural and construction corveé labor (Netherly, 1977:235). To mobilize both general and specialist labor, the lords

> "had the obligation to provide the implements—and for the planting, the seed—necessary for the task, in addition to food and drink for the workers" (Netherly, 1977:213).

Drink (*chicha*) was of particular importance: Netherly (1977:216–217) cites several documents in which the native informants say that without *chicha,* "the Indians would not obey their lords."

Chincha as a Coastal Economy: Ethnohistorical Model Two

Combining the data from the north coast and Chincha allows a more detailed reconstruction of coastal organization. Following are the principal features:

1. The population was divided into groups according to occupation. In addition to the farmers, fishermen, and merchants, there were a number of other, smaller specialist groups, such as the silversmiths. The large groups and those of the smaller ones requiring access to geographically restricted resources lived in their own settlements apart from the other groups.
2. Each group had its own lord or lords (depending on size).
3. The lords and their groups were organized into pairs, with one half of each pair subordinate to the other. This duality operated at several hierarchical levels; how it articulated with the Inka decimal organization is unclear. At the lowest level, pairs included different specialities. At the highest level was the paramount lord of the valley or polity. The Inka administrator was separate from this hierarchy.
4. Each group acquired the necessities which it did not produce by trading its products with the other groups (e.g., fishermen trading fish with the farmers for plant food or cotton). Some items may have circulated through state or local redistribution. The latter case is most likely when the Inka administrator or the local lords needed to mobilize general labor for farming or construction, or specialist labor to produce craft goods, *chicha,* etc., for the state.
5. Higher level lords (*caçiques principales*) often had some attached specialists, such as cooks, textile makers, and *chicha* makers, who produced the items required to maintain the lords' status.

This model corresponds to a large degree with the earlier version based strictly on the Chincha data; the differences arise a) from very specific Chincha data which are not treated in the north coast literature, such as the presence of long-distance traders or the use of copper money; or b) from the greater detail available in the north coast record concerning many aspects of organization, such as the asymmetrical pairing of *parcialidades* or the integration of the different specialists in such pairs. I have not repeated the information on the *mitimaes, yana,* or *aclla,* or on tribute to Cuzco, as these issues are general to all areas of the Inka empire, and are sufficiently documented in the Chincha record.

Combined with the specifically Chincha features of the first ethnohistoric reconstruction, the above model provides a system to be tested with the archaeological data on the Chincha fishermen presented in Chapters 5 through 11.

CHAPTER 3

SPECIALIZATION AND THE ARCHAEOLOGY OF CHINCHA FISHERMEN

Specialization was an important feature of all late pre-Hispanic Andean economies, both in the highlands and on the coast. Costin (1986:328) has recently defined specialization in this context as "the regular, repeated provision of some commodity or service in exchange for some other. These [commodities or services] may include productive resources, subsistence goods, craft items, or labor." According to the ethnohistoric record (Chapter 2), the primary commodity supplied by the Chincha fishermen was fish, a subsistence good, taken from the sea, a geographically restricted productive resource. The documents state clearly that the fishermen did not provide labor as a commodity. However, within the general rubric of specialization, there is room for significant variation. Part one of this chapter looks more closely at the parameters of this variation as seen in the two ethnohistoric models of fishing specialization presented in Chapter 2. Part two outlines the archaeological expectations for the Chincha fishing settlement, and part three discusses the archaeological methodology used in this study.

SPECIALIZATION

Following Brumfiel and Earle (1986), Costin (1986:330) defines

> "four parameters which characterize the organization of [specialized] production . . . (1) the context of production; (2) the relative geographic concentration of productive activities; (3) the constitution of productive units; and (4) the degree of specialization. Each of these parameters is actually a continuum between two opposite states."

For a detailed review of these parameters, the reader is referred to Costin (1986:Chapter VI) and Brumfiel and Earle (1986). Here, I locate the ethnohistorically described Chincha fishermen (Chapter 2) along these continua, first using Model One, which refers exclusively to Chincha, and then the more general Model Two, which incorporates the north coast record. A third alternative is that both ethnohistoric models are wrong and the fishermen were not specialists, or else they were specialized in a way not indicated by the documents.

For each of Costin's parameters, the two ethnohistoric models generate overlapping but not fully coincident sets of archaeological expectations; analysis of how the archaeological data from Lo Demás meet these expectations provides a powerful tool for contrasting and evaluating the two models.

Context of Production

The two states, or poles, of this parameter are independent and attached specialists. According to Brumfiel and Earle (1986:5):

> "*Independent specialists* produce goods or services for an unspecified demand crowd that varies according to economic, social, and political conditions. In contrast, *attached specialists* produce goods or provide services to a patron, typically either a social elite or a governing institution."

Following Model One, the Chincha fishermen are closest to the attached pole; they produced fish for tribute to a governing institution, the Inka empire. Although the fishermen probably originated as independent specialists, during the Late Horizon their status as specialist tribute-payers moved them towards the attached pole.

The situation of the fishermen in Model Two is more complex. First, they produced fish not only for tribute, but also for local exchange (like independent specialists) without the intermediacy of the governing institution. Second, the lords of the fishermen had their own attached specialists providing services and producing goods other than fish. In this model, the fishermen occupy several places simultaneously on the independent–attached continuum.

Concentration of Production

This parameter runs from dispersed to nucleated specialists. Costin (1986:336–337) defines the two poles of this continuum in the following way:

> "At one extreme are specialists who are evenly distributed among the population. . . . At the other extreme, specialists may be aggregated such that many producers or workshops are located at a single community within a region."

The Chincha fishermen in Model One clearly tend towards the nucleated pole; even though their settlement was geographically extensive, it was nucleated in political and economic terms. In Model Two, the fishing population as a single political and economic unit was nucleated as in Model One; however, *within* the fishing group were dispersed, nonfishing specialists—those attached to the fishing lords.

Constitution of Production Units

According to Costin (1986:338), "size and the principles of labor recruitment" are the variables which determine placement on this continuum.

> "Size reflects the actual number of individuals. . . . The principles of recruitment reflect the way producers are brought into the production system. At one extreme are small, family-based production units. At the other extreme are the wage-labor forces of the industrial west, where employment is contractual in nature and based on skill and availability" (Costin, 1986:338).

Model One offers little information on the principles of recruitment; the size of the fishing population—10,000 tribute-payers and their families—is quite large for a preindustrial society and would suggest placement of the Chincha fishermen towards the labor force side of the scale. However, the "Aviso" (Rostworowski, 1970:170) says that *each* fisherman went out with *his own* raft and nets, suggesting that the organization of fishing labor at the polity level was simply individual (family-based) organization multiplied many times.

Model Two is not relevant to the size of the Chincha fishing population. It does provide indirect evidence on labor recruitment; the use of a separate fishing dialect, *pescadora,* strongly suggests that fishing labor was recruited through social reproduction and not by contracting workers from a general pool.

Degree of Specialization

This parameter runs from part-time specialization, in which producers of basic subsistence goods produce commodities or provide labor in "spare" time, to full-time specialization, in which the producers of a particular good or service "work exclusively at one task, exchanging [this good or service] for all other goods and services used by the household" (Costin, 1986:342–343).

In terms of degree of specialization, the Chincha fishermen in Model One are located at the full-time specialists pole. The "Aviso" (Rostworowski, 1970: 170–171) states quite clearly that the only work they did was to fish. According to Model Two, however, the fishing lords had attached specialists (other than the fishermen), some of whom worked full time and some of whom worked part time.

Specialization Parameters and Archaeological Expectations for the Chincha Fishermen

Parameters of Specialization—Summary

The two ethnohistoric models of coastal organization (Chapter 2) place the fishermen of Chincha in somewhat different positions in terms of the parameters of specialization discussed above. In brief, according to Model One, the fishermen were attached specialists working for the state, concentrated in a nucleated community, with production units consisting of aggregates of individual producers, all of whom worked full time at fishing.[39]

Model Two differs from Model One because it recognizes more hierarchical levels within the fishing population. Thus, the fishermen in this model were still attached specialists in relation to the Inka state and probably to their local paramount lord, but at the same time, they were independent specialists in regards to their direct exchange of products with other local producers. In Model Two, the fishing population can also be seen as a small scale version of the polity or even the imperial structure, in that the fishing lords had their own attached specialists. Both models indicate a nucleated fishing population; Model Two, however, has a subdivision of this population into the fishermen and the other specialists attached to fishing lords. Units of production presumably still consisted of aggregates of individual fishermen working full time and recruited by birth, with the addition of the full- and/or part-time specialists attached to the lords.

Archaeological Expectations

According to Model One, the fishing settlement should be geographically discrete and should contain evidence only of fishing. As specialists attached to the paramount lord of Chincha and to the Inka state, the settlement should contain some evidence of links with these elites/governing institutions. Model One also specifies that the fishermen had their own lords, so the fishing settlement should include both elite and commoner sectors. With individuals or families as the basic units of production, the evidence for fishing should be evenly distributed throughout the settlement.

The archaeological expectations for Model Two are more complex. The fishing settlement should still 1) be geographically discrete, 2) have evidence of links with the governing institution(s), and 3) have elite and commoner sectors. Within the commoner sector, evidence for production should still be evenly dispersed, but in the elite sector, there should be evidence of the activities of specialists attached to the fishing lords, as well as of the activities of the lords themselves. In both models, all sectors should have evidence of exchange with other local specialists. There should be evidence of continuity through time in group identity.

To the extent that the archaeological data fit one or the other of the two sets of expectations, they will support either Model One or Model Two. To the extent that the data deviate from both sets of expectations, they will suggest problems with the ethnohistoric data. Deviations from these expectations could arise from two basic causes: 1) The fishermen were specialists, but their organization differed from that indicated by the documents (i.e., they occupied different places on the specialization continua than those listed in the previous section). The utility of the parameter approach is that it provides an open-ended set of alternative hypotheses to explain data which deviate from the models under consideration; or 2) The fishermen were not specialists.

Methodology for the Recognition of Specialization

Using the set of expectations discussed above requires a methodology for recognizing specialization in the archaeological record. Many archaeologists have approached this problem (e.g., papers in Brumfiel and Earle, eds., 1986); all of their methodologies rely on the contextual analysis of the tools of production and/or the products of the hypothesized specialists found in or on archaeological sites of various kinds.

In late pre-Hispanic coastal Peru, the presence or absence of specialization can be analyzed 1) by studying the artifact and utilized resource inventories at sites hypothesized to be specialized, with particular attention to intrasite distribution; 2) by comparing these inventories between contemporaneously occupied sites presumed to be of different specialists; and 3) by reconstructing the sites' locations at the time of occupation relative to arable land, rocky and sandy shoreline, and other resources.

For the Chincha fishing site, the artifact inventory should contain fishing tools such as nets and hooks; although not mentioned in the ethnohistoric documents, artifacts used in domestic activities (such as cooking pots) should also be present. Categories of tools used neither in fishing nor in domestic tasks would provide evidence of other production. The context of such tools would discriminate between specialists attached to the fishing lord (Model Two), nonspecialization of the fishermen (null hypothesis), or possibly dispersed specialization as described in the "concentration of production" parameter.

The utilized resource inventory of a specialist settlement should include a wide variety of products, among them items not produced by resident specialists. To fit Model One, detailed examination of the utilized resources in the fishing site should indicate that fishing products were processed by the site's inhabitants, but that other items were brought in in a processed state from elsewhere. Contemporary nonfishing sites should have a qualitatively similar assemblage, but one that indicates a productive activity other than fishing. As with the artifact inventory, the utilized resource inventory can serve to discriminate between the alternative models for the specialization of the fishermen; depending on context, the presence of processing by-products of materials other than fish can provide evidence for specialists attached to the fishing lords, for nonspecialization of the fishermen, or for a dispersed pattern of specialization. The absence of such products anywhere in the fishing site would support the strict specialization model (Model One).

Another crucial issue is the difference between what Muller (1986:15) has referred to as " 'site specialization' (limited activity sites) and actual 'producer specialization'." Both ethnohistoric models for the Chincha fishermen clearly describe producer specialization; to test for this aspect of the models, it is necessary to show that the fishing site was not a limited activity area, i.e., that it was occupied year-round and that its inhabitants carried out a full range of domestic activities in addition to their specialized production. Evidence for domestic activities would include dwellings, cooking vessels, food remains, etc. Year-round occupation can possibly be checked through analysis of organic and other remains (Rafferty, 1985:129–137), though this has seldom been done on the Andean coast (*see* Griffis, 1971, for one attempt). The depositional history at a site can also provide clues to seasonality in environments in which seasonal abandonment would produce a characteristic deposit such as wind-blown sand (*see* Chapter 5).

A final procedural point involves data gathering. The two basic choices are surface collecting and excavating. Each has advantages and drawbacks, and the choice of approach must be tailored to the research problem, to the specific methodology to be used, and to the conditions of the individual site or region. Surface collecting (e.g., Brumfiel, 1980) is useful only if the analytic procedure involves tools but not organic remains, and if the conditions of preservation are such that reliable associations can be found in surface contexts. The advantage of surface collecting is that large areas can be covered quickly and inexpensively.

Excavating provides better contexts and, depending on the choice of site-type, a wider range of materials including organic remains. Burials can provide good collections of tools; in the Andes, it is likely that tools were buried with their users, and analysis of the bodies can corroborate conclusions concerning an individual's activities during life. However, burials are unlikely to provide processing debris or other direct evidence of daily life. Another drawback to burials is that a study of specialization requires a cemetery with a large population and good preservation. Workshops and habitation areas provide good context, temporal control, and a wide variety of materials. The primary disadvantage of such sites is that they are time-consuming and expensive to excavate and analyze. Thus, studies based on workshop/habitation site excavation tend to suffer from limited sample size. Nevertheless, the methodology used in this study requires samples of organic remains and artifacts and secure context for all materials; workshop/habitation site excavation was selected as most appropriate.

CHAPTER 4

THE ARCHAEOLOGY OF CHINCHA

The Chincha Valley

The Chincha valley is located on the Peruvian coast about 200 km south of Lima, between approximately 13°20′ and 13°35′ south latitude and 76°00′ and 76°12′ west longitude (Fig. 1). The valley is part of Chincha Province, the northernmost province of Ica Department.

The Chincha valley is watered by the San Juan River, which exits from bedrock 20 km east of the shoreline and splits into two branches, the Río Chico to the north and the Río Matagente to the south (Fig. 1). The bifurcation of the San Juan marks the beginning of the lower valley; the following descriptions refer only to the lower valley, the area of concern in this study, and the meteorological data are from a station which is geographically analagous to Lo Demás, the Chincha fishing site.

From less than 2 km wide at the bifurcation of the San Juan River, the Chincha valley opens abruptly to more than 15 km at the shoreline. Based on aerial photographs taken in 1962 and field work carried out in the 1960s, the total area of the valley was calculated as 30,716 hectares, of which 22,247 (72.4%) were in agricultural use at the time of the study (ONERN, 1970, Volume II:Map 5). According to Romero (1953:96, cited by Menzel and Rowe, 1966:70), at midcentury Chincha ranked sixth among all Peruvian valleys and first among those south of Lima in terms of agricultural production.

Both of the distributaries of the Río San Juan (the ríos Chico and Matagente) are seasonal, with significant flow only in the Peruvian summer (December to April); both branches are often dry during the rest of the year (ONERN, 1970, Volume II:58). The lower Chincha valley lies wholly within the Pre-Montane Desert ecological formation (ONERN, 1970, Volume I:47–48, Map 2). General characteristics of this formation include an arid to "semi-*calido*" climate; irrigation required year-round for agriculture; alluvial, colluvial, and lithosolic soils; and variable topography (ONERN, 1970, Volume I:46). The average annual temperature in the lower valley is 19.1°C, with a peak around 23°C in January to March and a low of 17° to 18°C from June through October. In the absence of an El Niño event, average annual precipitation is 0 mm, though the average annual relative humidity is 81% (ONERN, 1970, Volume II:10–12 and Map 1).

According to the ONERN study (1970, Volume I:68–69, Map 2), the lower Chincha valley is completely covered with Quaternary deposits. The central portion of the lower valley, around the Río Chico and the Río Matagente, is composed of Holocene channel and floodplain deposits. On the north side of the valley, from about a kilometer north of Tambo de Mora to the Quebrada Topará, the Pleistocene Topará Formation of intercalated sands and clays crops out in a 6 to 8 km wide belt. The west face of this outcrop forms a 30 m or higher bluff that may mark a north–south trending fault; the beach lies less than a kilometer to the west. A bluff also delimits the Topará Formation on the south, overlooking the floodplain. The area covered by this formation is referred to locally as the *meseta* or tableland of Chincha Alta. Inland from the Topará Formation and on the southern edge of the valley are Quaternary alluvial deposits.

The modern population center in the valley is the town of Chincha Alta, located on the north side of the valley about 5 km from the shore (Fig. 1). Other important modern settlements include the port of Tambo de Mora, Chincha Baja, and El Carmen.

History of Archaeological Research in Chincha

Archaeological research in the Chincha valley began in 1901 with Max Uhle's excavation of late pre-Hispanic burials at six sites (A to F, Kroeber and Strong, 1924:Plate 1) in the general vicinity of Tambo de Mora and along the edge of the Topará Formation (Kroeber and Strong, 1924; Uhle, 1924). Uhle's final report on the Chincha excavations was never published, but a field report written in 1901 is available (Uhle, 1924). Kroeber and Strong (1924: 3–8) gleaned further information on the sites and the excavations from Uhle's field catalog.

Following Uhle's pioneering work, no published archaeological field investigations were carried out in Chincha until the late 1950s. However, during the interim, several scholars worked with materials from Uhle's Chincha collection; Kroeber and Strong (1924:9–54) published their analysis of the artifacts (except textiles); O'Neale et al. (1949) published their study of Chincha burial textiles; Carter (1945) identified some cucurbit and gourd seeds; and Whitaker

(1948) described and illustrated gourd vessels. Also during this interval, Julio C. Tello visited the ruins of "La Centinela, Kumbe [sic], and San Luis" in the Chincha valley in October, 1915 (Guerrero, 1984: 2). Ten years later, in 1925, Tello returned to Chincha during his Second Archaeological Expedition to the South (Guerrero, 1984:3). The results of Tello's studies in Chincha have never been published.

Wallace (1971:*passim*) indicates that Lawrence E. Dawson had recorded some sites in the Chincha valley in 1955. In 1957 and 1958, Wallace carried out a surface survey of Chincha as part of the Peruvian Fulbright Program's archaeological project of the late 1950s (Menzel, 1971; Wallace, 1959, 1971). During the survey, Wallace recorded a total of 111 archaeological sites (cf. Sandweiss, 1989:68, note 58) ranging in date from the Early Horizon to the Initial Colonial Period (Wallace, 1971:4–80, 1972). Although most of the lower valley was covered, only a small part of the *meseta* of Chincha Alta on the north side of the valley was surveyed. In a mimeographed article (Wallace, 1972) accompanying his survey data (Wallace, 1971), Wallace elaborated on his earlier published version (Wallace, 1959) of the cultural sequence in Chincha; this work was the first synthesis of Chincha prehistory that dealt with the periods predating the Late Intermediate Period, although Uhle (1924:51–54) and Kroeber and Strong (1924:51–54) had identified a small number of sherds recovered around Site D (PV 57–10) (*see* Fig. 1) as pertaining to an earlier culture (Kroeber and Strong, 1924:Plate 1). Kroeber and Strong called this culture "Proto-Chincha."

Only two excavations were carried out in Chincha during the Fulbright project, both at Early Horizon sites. As Menzel (1971:97–98) explains, the main objective of the Fulbright project was to establish chronological sequences for the Peruvian coastal valleys, and Wallace had several reasons for concentrating on the early ceramic periods. Thus, Wallace dug a small test pit at site PV 57–63 to increase the collection of Early Horizon Pinta phase ceramics, and he dug a 2 × 3 m test pit together with Edward P. Lanning at the Early Horizon Pozuelo phase type site (PV 57–52) on the southern side of the valley (Lanning, 1960:412–423; Menzel, 1971: 101; Wallace, 1972) (*see* Fig. 1). In 1956, Lanning had excavated at the Early Horizon Jahuay site at the mouth of the Topará *quebrada,* to the north of Chincha, providing a background for the discoveries by Wallace (*see* Fig. 1).

During the next two decades, from 1959 to 1983, published research into Chincha prehistory again focused on the analysis of materials from earlier projects, and no new field work was carried out. In 1966, Menzel published her study of the late Chincha pottery from the Uhle collections. In the same volume of Ñawpa Pacha, she and Rowe drew on that work, Wallace's survey, Menzel's study of late Ica pottery (later published as Menzel, 1976), and historical sources to reconstruct the "role of Chincha in late pre-Spanish Peru" (Menzel and Rowe, 1966). In 1967, Menzel again utilized the Uhle Chincha collections in her article on late Ica figurines.

In 1971, Spanish translations of both Wallace's survey of Chincha and Menzel's 1960 summary of the Fulbright studies on the south coast appeared in Peru (Menzel, 1971; Wallace, 1971). Menzel's version of the cultural sequence is essentially the same as Wallace's account, as both are based primarily on Wallace's field study. Chincha also receives some mention in Menzel's analysis of late pre-Hispanic ceramics from the Ica valley (Menzel, 1976). During the 1970s, Garaventa (1979) restudied some of the Chincha burial textiles excavated by Uhle and originally examined by O'Neale et al. (1949). Recently, Wallace (1985, 1986, 1991) has published re-studies of his 1950s material, elaborating on the Early Horizon and early Early Intermediate Period of the south coast, including Chincha, and on the late pre-Hispanic Chincha road system.

Another important advance in the study of Chincha prehistory and protohistory in the last two decades has come from the publication and analysis of ethnohistoric documents relating to the valley in late pre-Hispanic times (*see* Chapter 2).

The ongoing Chincha–Pisco Archaeological–Historical Project began field work in the Chincha valley in 1983 under the joint direction of Craig Morris, Heather Lechtman, Luís Lumbreras, and María Rostworowski. This project has involved archival research, resurvey of the valley, and excavation and mapping at several sites, including the Inka and Chincha administrative center at La Centinela (PV 57–1) and the late pre-Hispanic farming site of Huacarones (PV 57–91) (*see* Fig. 1). My research on the late pre-Hispanic fishermen of Chincha has been done in association with the Chincha–Pisco Project. During the same period of time, a German expedition has been surveying, mapping, and doing limited excavation in the neighboring Quebrada de Topará, with a primary focus on late pre-Hispanic burial sites (Wurster, 1986). These new studies

Colonial Period		
		1532 A.D.
Late Horizon	post-Chincha assemblage/ Chincha style	1476
Late Intermediate Period	Chincha style? Chulpaca C Chulpaca B	1000
Middle Horizon	Nuevo Estilo (Huacarones)	
		500
Early Intermediate Period	Estrella Carmen Campana --------------------- Chongos	0 A.D./B.C.
	Topará Tradition	
Early Horizon	Jahuay 3 San Pablo -------------------	
	Pinta ----------------------- Paracas Tradition Pozuelo -----------------------	500
Initial Period		1000 B.C.

Fig. 2.—Chronological sequence for the Chincha valley. Dates before the Late Horizon are approximate. Based on data from Lumbreras (1985), Menzel (1966, 1971, 1976), Menzel and Rowe (1966), and Wallace (1971, 1972, 1985, 1986).

should soon lead to a more detailed picture of Chincha culture history; based on the first several seasons of field work by the Chincha–Pisco Project (particularly the resurvey of the valley by Lumbreras), an updated synthesis of Chincha prehistory is already available (Lumbreras, 1985).

Culture History of the Chincha Valley

Fig. 2 summarizes current knowledge concerning the prehistoric sequence of the Chincha valley. The phases from Pozuelo through Estrella are those originally defined by Wallace (1959, 1972) based on his analysis of Chincha ceramics. Lumbreras (1985) has proposed Huacarones as the phase name for one of the "Nuevo Estilo" (New Style) Middle Horizon variants recently found by him in the valley. The earliest Spanish documents (e.g., Samano-Xerez, 1967 [1527–1528]; Cieza, 1984 [1550]:218–221, Cap. LXXIII) record the name "Chincha" in reference both to the valley and to its indigenous inhabitants; since Uhle's time, the name has also been used to refer to the late pre-Hispanic culture of the area.

In terms of absolute chronology, the only radiocarbon dates from the Chincha valley are those reported in this study for the Late Horizon site of Lo Demás (*see* Chapters 5 and 11). All of the period attributions in the left hand column of Fig. 2 were derived from ceramic affiliations with neighboring valleys of the central and south coasts. The absolute dates are those commonly accepted for the major ceramic periods and horizons of Peru; no preceramic sites have been identified in Chincha.

Detailed descriptions of the ceramic styles that define the different phases are found in Menzel (1971) for the Early Horizon through middle Late Intermediate Period pottery and in Menzel (1966) for the later Late Intermediate Period and Late Horizon ceramics. Additional information on ceramics of all phases is available in Wallace (1972); his more recent articles provide more details for the Pinta (Paracas) (Wallace, 1985) and Topará pottery (Wallace, 1986). Further consideration of the late pre-Hispanic pottery of Chincha is found in Chapter 7 of this study. Sandweiss (1989) synthesized the available data on the culture history of Chincha from the earliest known occupation (Early Horizon) through the Middle Horizon. Following is a background summary of the late pre-Hispanic periods in Chincha.

The Late Pre-Hispanic Periods in the Chincha Valley

The majority of archaeological information available for Chincha concerns the late pre-Hispanic periods (Late Intermediate Period and Late Horizon), when the most intensive occupation of the valley took place. According to Menzel and Rowe (1966:70), late pre-Hispanic time in the Chincha valley is characterized by increasing autonomy of the indigenous Chincha culture. This process continued until the Inka conquest and domination (but not destruction) of Chincha in the later Late Horizon, during which time Chincha "maintained its prestige." More sites and more kinds of sites date to these late periods than to any earlier period, and the entire valley was occupied with the exception of the southern edge. The largest sites in the valley were built during the late pre-Hispanic periods, among them El Cumbe (PV 57–3), the San Pedro complex (PV 57–7), Huaca Tambo de Mora (PV 57–2), and the Chincha and Inka administrative center at La Centinela (PV 57–1) (Morris, 1988; Santillana, 1984; Wallace, 1971, 1972) (*see* Fig. 1). Wallace (1972:3) considers some of the large sites to be planned centers with special functions, but states that many are habitation sites composed of one or more high mounds built through "the accumulation of garbage and the rubble from earlier buildings." According to the number and size of the mounds, Wallace classifies these sites as small urban centers, large towns, small towns (villages), and rooms occupied by extended families which, if the walls are high and well made, might be considered as palaces or religious structures.

Wallace (1972:3–4) found that the large late sites of Chincha cultural affiliation were made of *tapia* (puddled mud and/or rammed earth), while Inka constructions in the valley had large, rectangular *adobes* (mud bricks) "with measurements in imitation of the rectangular stones [used by the Inka] in highland structures." Santillana (1984:28–29) lists three combinations of *adobes* and *tapia* found in Chincha culture and "bilateral" (Inka/Chincha) sectors at La Centinela, the Chincha and Inka administrative center: 1) *tapia* on *adobe*; 2) *adobe* on *tapia*; and 3) horizontally alternating *tapia–adobe–tapia.* The first type was found in a sector considered to have both Chincha and Inka occupations. The next two cases occur in predominantly Chincha sectors. Type 2 involves small, "lightly rectangular" *adobes* that seem to have been added slightly after the *tapia* construction by local people working to Inka specifications. The third type seems to occur only when *adobes* were used to fix gaps in earlier *tapia* walls. The purely Inka sectors of the site are built of rectangular *adobes,* as Wallace noted. At El Cumbe, Uhle (1924:67) observed a façade of "small boulders" covering the natural strata of the main mound; these cobbles are still visible in places. In the Late Horizon fishing site of Lo Demás, walls in Sector I (an area of common residences) were made of cobbles set in mud mortar (*see* Chapter 6). Sector I of Lo Demás lies about 100 m from the western edge of El Cumbe.

Another interesting feature identified by Wallace (1972:3, 1991) in apparent association with the late sites is a series of roads radiating out from La Centinela; some of these roads are "more notable in the aerial photographs of the valley than the Panamerican [highway]" (Wallace, 1972:3). The roads connect many of the largest late sites in the Chincha valley; one runs parallel to the shore from La Centinela to the San Pedro group. Because of the symmetry of the system—the roads running east and south from La Centinela form a right angle divided evenly into thirds by two diagonal roads—Wallace (1972) initially argued that the plan must be ceremonial. However, it is worth recalling that the "Aviso" document (Rostworowski, 1970; *see* Chapter 2) describes the Chincha fishing settlement as "looking like a beautiful and long street." Furthermore, Rostworowski (1981:86) has found historic evidence from the Colonial Period concerning fishermen's roads in the central coast Lurin valley; there were five roads, of which the two closest to the sea were used by fishermen in their roles as messengers and as fishermen, respectively. Whether or not the Chincha roads had a purely ceremonial function remains to be demonstrated; however, Wallace himself (1991) has recently suggested multiple (including ceremonial) functions, based in part on the ethnohistoric data.

Using both ethnohistoric and archaeological data, Menzel and Rowe (1966) sketched the history of the Chincha valley during the Late Intermediate Period and Late Horizon. During the first half of the Late Intermediate Period, the inhabitants of Chincha were much influenced by their neighbors in the Ica valley to the south. The evidence for this influence is the presence of the Ica pottery style *Chulpaca B* and both imported and local versions of the later *Chulpaca C* pottery (Menzel, 1971:137). The two Chulpaca styles found in Chincha date to the first half of the Late Intermediate Period, and Menzel (1971) suggests that Ica influence on Chincha was strong during both phases despite a relative decline during Chulpaca C.

The assertion of local stylistic (and political?) autonomy first seen in the production of local variants of Chulpaca C pottery continued in the following phase, *Chincha-Soniche,* which Menzel (1971:137–138) considers as a local derivation out of Chulpaca C. Chincha-Soniche developed into the *Chincha* style proper[40] (Menzel, 1971) during Late Intermediate Period 8 and the early Late Horizon (prior to the Inka conquest of Chincha) (Menzel, 1966:65–66).[41] At this time, Menzel and Rowe (1966) find strong Chincha influence in the pottery of Ica and interpret it as evidence that the Chincha polity dominated the south coast region centered around the Paracas Peninsula. Chincha style pottery, meanwhile, "had closer relations with the north than with Ica . . . resembl[ing] very closely the corresponding pottery of Cañete and, less closely, that of the central coast. The resemblances extend to the valley of Chancay" (Menzel and Rowe, 1966:65; *see also* Menzel, 1966).

Most of the large, late sites in Chincha were built or at least in use during the Chincha phase. Although the presence of obvious Inka structures at La Centinela (*see below*) led Uhle (1924:72–75) to believe that the whole site was Inka (he thought that the main pyramid, a Chincha structure, was an Incaic Temple of the Sun), Wallace (1971:5) found Late Chincha ceramics and friezes as well as Inka potsherds at the site. Menzel and Rowe (1966:66) suggest that La Centinela formed a pre-Inka complex with the nearby Huaca de Tambo de Mora and El Cumbe, and that it was the capital of the Chincha polity. Recent work at La Centinela has confirmed the presence of both Chincha and Inka sectors at the site (Morris, 1988; Santillana, 1984). However, Santillana's (1984) study is based on architecture and surface collections. Considering the probability that Chincha style ceramics (and architecture?) continued in use throughout the Late Horizon, it is unclear whether or to what degree the Chincha and Inka sectors of La Centinela differ chronologically.

Uhle (1924:64–66) found both Late Chincha and Inka sherds around the Huaca de Tambo de Mora, and he argued that this site was the palace of the principal lord of Chincha. He also reasoned (by analogy to Pachacamac, the great coastal oracle–shrine in the Lurin valley near Lima) that El Cumbe was the temple of the Chincha creator god Chinchaycamac (Uhle, 1924:67–69). Uhle's argument concerns the relation of the main mound of the site with Cemetery B (PV 57–6)—this burial ground lies at the foot of the mound on its western side, as does the cemetery at Pachacamac. As Uhle points out, Chinchaycamac was considered to be a "daughter" or branch oracle of Pachacamac (*see* Chapter 2; *also* Patterson, 1985). However, Uhle also noted that the pottery from the Chincha cemetery dated only to the last pre-Inka period (as Kroeber and Strong [1924] and Menzel [1966] also found in their analyses of the ceramics from Cemetery B, but cf. note 41). Uhle concluded that El Cumbe and Cemetery B were a sacred precinct in use at the time of the Inka conquest of Chincha and that the Inkas destroyed this sanctuary.[42]

By the time the Inka conquered Chincha ca. 1476 (Menzel and Rowe, 1966:67), Chincha seems to have developed a highly centralized government that directly controlled both the Chincha valley and the northern half of the Pisco valley and strongly influenced the Ica valley. The Inka under Thupa Yupanki apparently conquered Chincha without a fight and made it into an administrative province separate from Pisco and Ica, an "arrangement [that] reduced the local influence of Chincha" (Menzel and Rowe, 1966) (*see* Chapter 2). However, as argued in Chapter 2, the *long-distance* influence of Chincha may have grown under Inka rule as a result of increased long-distance trading.

According to Menzel (1966), the later Late Horizon in Chincha, after the Inka conquest of the valley, is marked by the *post-Chincha pottery assemblage* (but *see* note 41), which is equivalent to Kroeber and Strong's (1924) Late Chincha II and Inka pottery (Menzel, 1966:121; Menzel and Rowe, 1966:64). This assemblage includes some pottery derived from the Chincha style, a relatively large proportion of imported foreign pottery (mostly from the central coast), and Inka and Chincha–Inka pottery. The importance of the central coast ceramics in the post-Chincha assemblage is explained by the fact that "Chincha had a double allegiance during the period it was under Inca rule; it was not only subject to the Inca government but also to the oracle of Pachacamac" (Menzel and Rowe, 1966:68). Because of an agreement made with Thupa Yupanki, the priests of Pachacamac were allowed to establish branch oracles in various places including Chincha (*see* note 42). This arrangement gave the priests political power in the valley during the period of Inka rule (Menzel and Rowe, 1966). Patterson (1985:164) suggests that the branch oracle in Chincha (Uhle's "daughter" of Pachacamac) was actually established shortly before the Inka conquest of the valley, and that one of its functions was to provide the Inka with information about Chincha. He also notes that "the caretakers of Pachacamac and the Incas were closely linked in those areas [such as Chincha] that were beyond the imperial frontiers when the branch oracles were established in them" (Patterson, 1985: 168). This observation accords well with the importance of central coast wares in Late Horizon Chincha and their association there with Inka pottery (Menzel, 1966:120–125).

The Inka established their administrative center for Chincha at La Centinela, a large part of which consists of *adobe* structures (a coastal trait) built according to the highland Inka architectural canon, including trapezoidal doorways and niches. Much of the Inka pottery from the Uhle collections came from Cemetery E (PV 57–11), the closest burial ground to La Centinela (Kroeber and Strong, 1924: Plate 1; Menzel, 1966:122). The Inka presence in Chincha is most obvious at these two sites, but there are a few other traces in the valley. Wallace (1972: 4) notes the presence of the rectangular *adobes* "always associated with Incaic features" in the large platform (A) at the San Pedro complex on the south side of the valley (Wallace, 1971:9). Wallace did not collect any Inka sherds at this site, but on one of the other San Pedro mounds, I found a fragment that C. Morris identified in the field as Ica–Inka. Inka pottery is known from some other sites, including Lo Demás (*see* Chapter 7).

The ethnohistoric evidence concerning the economic and social organization of late pre-Hispanic Chincha has already been discussed in Chapter 2. Of central importance are the indications that the population of Chincha was divided into residentially discrete and occupationally specialized groups, principally laborers (mostly farmers), fishermen, and merchants (Rostworowski, 1970). Long distance trade by land and sea was particularly important. Rostworowski (1970) believes that this pattern of occupational specialization and residential separation predates the Inka conquest of Chincha, and that the Inkas allowed the Chincha to retain their economic organization despite the fact that this system differed significantly from the highland Inka system (Murra, 1972, 1980). Conquered groups were not always allowed such freedom, and Rostworowski (1970) feels that the Chincha were accorded this privilege because of the importance of the maritime trade to the Inka empire. Unfortunately for this interpretation, few specimens of the imported Ecuadorian *Spondylus* shell have been found in Chincha; Rostworowski (1970), Murra (1975), and others believe that *Spondylus* was the principal trade item acquired by the Chincha merchants. Uhle found no *Spondylus* shells in Chincha (Late Chincha I) graves, and from two to five of the shells in each of four graves of the post-Chincha assemblage (Late Chincha II and Inka) (Kroeber and Strong, 1924:30). In Chincha, *Spondylus* is not often found on the surface of looted sites nor in local antiquities collections, unlike the situation in the Moche valley on the north coast, where *Spondylus* is extremely common. Only a few fragments of this species occurred at Lo Demás (*see* Chapter 9). As suggested in Chapter 2, Chincha merchants may not have participated in extensive long-distance trade to the north until (and as a result of) their incorporation into the Inka empire.

The earliest Spanish presence in Chincha dates to 1534, only two years after the arrival of the Spaniards in Peru. By 1542, a Dominican monastery had been founded in the valley. Perhaps because of the early presence of the Europeans, the indigenous population of Chincha declined even more rapidly than in other coastal valleys (Menzel and Rowe, 1966; Rostworowski, 1970). Cook (1981:160) calculates a ratio of population decline for Chincha of 100:1 for the first 85 years after the Spanish conquest. In historic times, the valley has often been prosperous but was never again a major maritime center, either in terms of fishing or trade, until the *anchoveta* boom in the 1960s. With the drastic decline in *anchoveta* capture following the 1972–1973 El Niño event, fishing is once more a minor part of the Chincha economy.

CHAPTER 5

LO DEMÁS: DESCRIPTION AND EXCAVATIONS

The Site of Lo Demás

The Discovery of Lo Demás

The archaeological criteria for the Chincha fishermen's settlement described in the "Aviso" document (Chapter 2) are 1) location near the shore in the Chincha valley, 2) late pre-Hispanic date, and 3) evidence of fishing. Any site meeting these criteria would have to be considered as part of the specialized fishing settlement; the ethnohistoric models of Chincha economic organization presented in Chapter 2 can be evaluated by analysis of such a site in terms of the expectations listed in Chapter 3.

The "Aviso" document (Rostworowski, 1970: 170–171) describes the fishing settlement as looking like a road ("parecía una calle hermosa y larga") running along the shore ("por la costa de la mar"). This "road" began two leagues (one league is approximately five km, *see* Hyslop, 1984:295–296) before arriving in Chincha (probably the site of La Centinela; *see* Fig. 1), had a total length of five leagues, and reached a place called Lurinchincha. During June and July of 1983, I visited sites along the Chincha coast beginning on the southern side around the former Hacienda Lurinchincha (Fig. 1). Although late pre-Hispanic mound groups are preserved there (Chapter 4), intensive agriculture has removed obvious traces of small-scale residential sites throughout the entire valley floor; I was unable to locate any sites that might have been common fishermen's dwellings in that zone. On the north side of the valley, however, on the seaward side of the Chincha Alta *meseta* (*see* Chapter 4), Peruvian archaeologist Idilio Santillana found a number of net fragments on the surface of an area where a deep quebrada precludes irrigation and concomitant agriculture. This site parallels the shoreline, and its long, narrow form resembles a road.

On inspection, I found archaeological deposits exposed in the quebrada profile of the southern sector of the site. The strata contained abundant remains of fish and plants, along with late pre-Hispanic potsherds, net fragments, textiles, and other artifacts. Cobble and mud mortar walls, clay and earth floors, and hearths were visible. Other sectors had evidence of burials and of large scale structures. Clearly, this site met the criteria for a suitable place to test the ethnohistoric data on the Chincha fishermen (and, for reasons of preservation, it appeared to be the only large section of late pre-Hispanic fishing settlement available for study in the valley). The site lacked a local designation, so I named it "Lo Demás" from the "Aviso" document's description of the fishermen's daily lives (*see* Chapter 2).

Modern Site Environment and Description

The site of Lo Demás is located on the northern side of the Chincha valley, about 250 m west of El Cumbe (PV 57–3) and 725 m west northwest of the Chincha and Inka capital at La Centinela (PV 57–1) (Figs. 1, 3). The present-day fishing village of Tambo de Mora lies 1.2 km to the southwest of Lo Demás, while Chincha Alta, the provincial capital, is 5 km to the east and north. The site is situated at an average height of about 40 m above sea level, on top of the southwestern edge of the Chincha Alta *meseta*.

Lo Demás today is an unoccupied, unvegetated strip of sandy desert. This condition has apparently characterized the site since the Spanish conquest or shortly thereafter, given the lack of substantial Hispanic-era deposits and the excellent preservation of the late pre-Hispanic organic remains. Had the site been irrigated at any time following the final pre-Hispanic occupation, the organic remains would not be so well preserved. Lo Demás lies on a major path connecting settlements on the Chincha Alta *meseta* with the lowlands of the lower valley around Tambo de Mora and Chincha Baja, and the only recent deposits at the site are superficial traces left by the people, sheep, goats, horses, and burros who frequent the path.

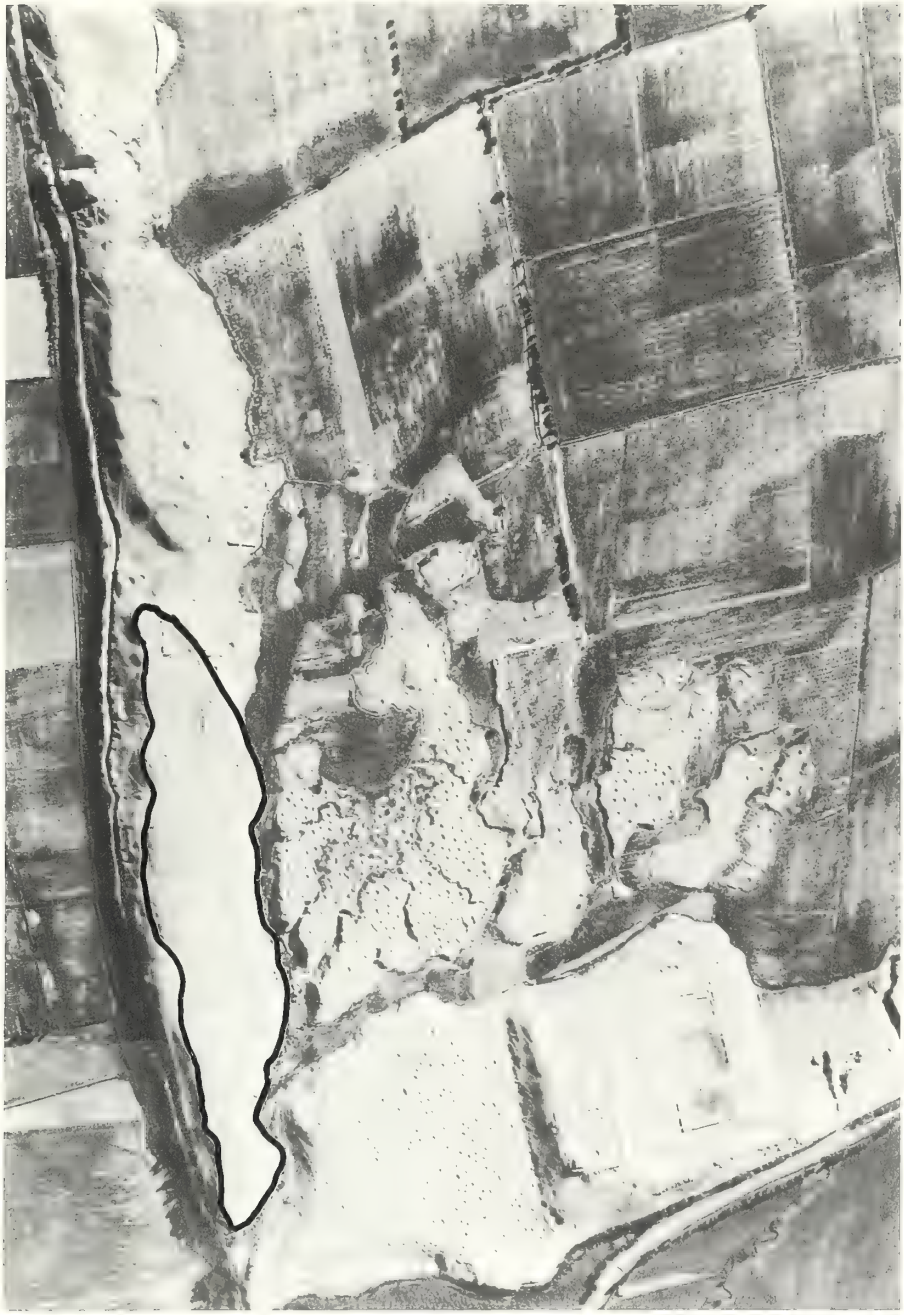

Fig. 3.—Aerial photograph of Lo Demás and immediate vicinity. North is at the top of the photograph. The intact portion of the site is outlined in black; note the monumental structures just north of the intact zone. The pockmarked zone to the right (east) of Lo Demás is the heavily looted Cemetery B (PV 57–6); the rectangular structure to the right of Cemetery B is El Cumbe (PV 57–3).

Lo Demás runs parallel to the shoreline and overlooks the sea some 900 m to the west. A sheer bluff borders the site on its western, seaward side and at its southern terminus; a modern irrigation canal runs along the side of the bluff below the site (Fig. 4). At the base are agricultural fields, planted mostly in cotton to the west and maize and garden crops to the south. A modern road runs along the western edge of the cotton fields, separating them from a strip of sandy beach.

To the north of Lo Demás, the surface of the bluff dips slightly before continuing northward. Many

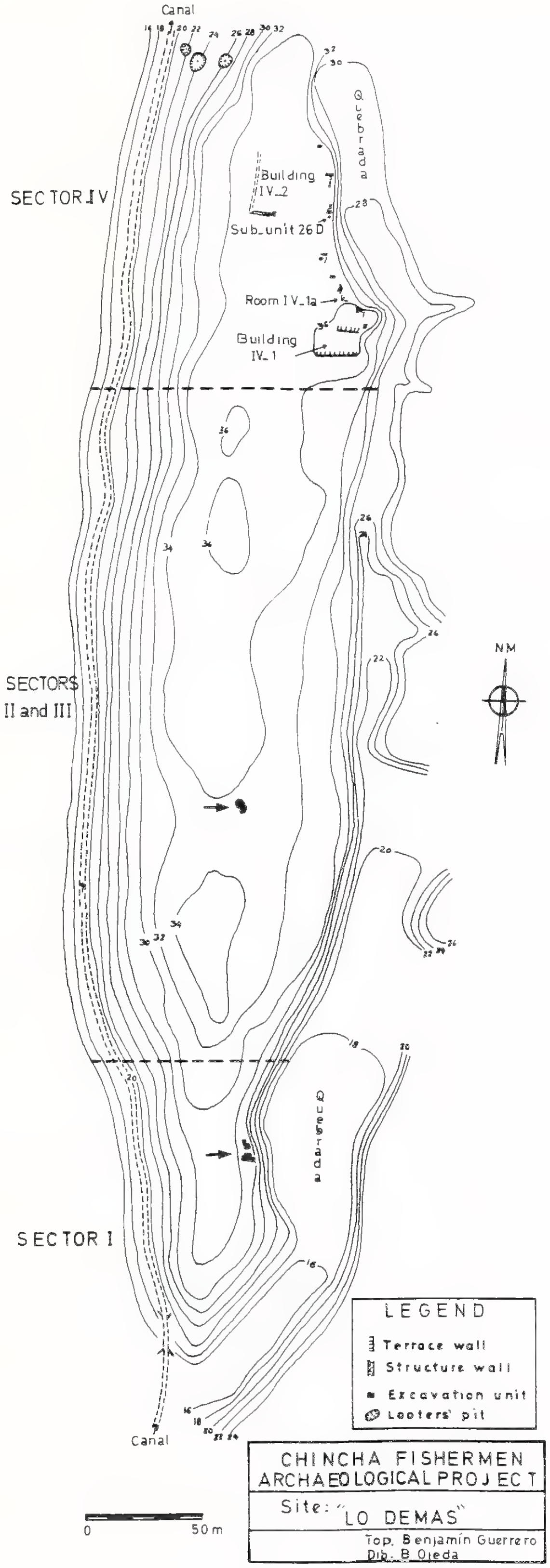

Fig. 4.—Lo Demás site map, showing division into sectors and location of excavations. Arrows point to excavation areas.

quebradas cut through the bluff, most notably the Quebrada de Topará near the Jahuay beach, some 15 km from Lo Demás. Just north of Topará, the bluff rises and the adjacent beach disappears.

A quebrada runs along the eastern side of Lo Demás, separating the site from a late pre-Hispanic cemetery (PV 57–6, Uhle's Cemetery B [Kroeber and Strong, 1924]) at the foot of El Cumbe. The latter site is a large, artificial mound thought to date to the late pre-Hispanic periods (Fig. 3) (*see* Chapter 4).

Although irrigation runoff flowing through the quebrada continues to erode the eastern margin of the site, the geographic impediments noted in the preceding paragraphs isolate the surface of Lo Demás from running water. Consequently, Lo Demás has been spared from the intensive irrigation agriculture that has destroyed most of the pre-Hispanic residential sites in the lower Chincha valley. This fact and the extreme aridity of the Peruvian coast account for the excellent preservation of organic and other remains.

Archaeological strata are exposed along much of the eastern profile of Lo Demás, where the site has been sliced open by the quebrada. However, the surface of Lo Demás is remarkably clean, considering the extensive archaeological deposits that underlie the entire site: few remains are found exposed on the surface of the site, except around recently looted burials. This condition is due largely to salitrification (precipitation of salts from the atmosphere) and to the strong winds which blow over the site from the southwest, particularly in the *paracas* season during September and October (Cánepa P., 1982:16). In late August, 1983, these winds were strong enough to fill the excavation pits with four cm of sand during a single night. Salitrification weakens the artifacts and organic remains, and the windblown sand either buries or destroys them. Fairly thick sand deposits have accumulated in some parts of the site, but there are also windscoured areas of Lo Demás where in situ archaeological deposits begin less than a centimeter below the surface. The difference depends on the nature of the original structures; sand accumulates in and around unfilled rooms, but blows across rooms filled with primary midden or construction material.

Site Environment During the Late Pre-Hispanic Occupation

At the time Lo Demás was occupied, the site and its surrounding environment were somewhat different than at present. As recently as 1901, sketch maps by Uhle (1924:Plates 1 and 24) indicate that the area to the west and south of the site was marsh. This information is consistent with the presence of marsh species among the plant remains recovered from Lo Demás (*see* Chapter 10). To the north of the present site limit, 1942 aerial photographs reveal that the two extant buildings in the northern sector of Lo Demás (Sector IV, *see below*) formed only part of a more extensive area of monumental architecture containing at least two other large structures (Fig. 3). Today, none of these other buildings remain, and the area north of the site is now a vineyard. According to local informants, the structures were bulldozed in the early 1970s. The remaining buildings, a stepped mound and a rectangular enclosure, have been severely eroded along their eastern margin by the quebrada; runoff from the vineyard has probably increased the rate of erosion over the last decade. A meter-wide slice of Building IV–2 disintegrated into the quebrada between August 1985 and September 1986.

At the time Lo Demás was occupied, the quebrada to the east ran along part of its present course opposite the southern half of the site, separating it from Cemetery B. The midden deposits in the southeastern corner of Lo Demás overlie the former quebrada edge, as do midden strata associated with the southwestern sector of Cemetery B. Deposition by the late pre-Hispanic inhabitants of Lo Demás gradually filled in part of the quebrada (*see* Chapter 6).

Opposite the middle of the site, a series of small quebradas enter the main, east–west channel. At some time in the past, these lateral gullies were filled by flood deposits and are now being exhumed by irrigation runoff (Sandweiss, 1989:107). The flood which filled the quebradas was probably part of a post-Columbian El Niño event, in which case the lateral quebradas existed during the late pre-Hispanic occupation of Lo Demás (Sandweiss, 1989: Appendix A).

Across the quebrada, the lands bordering Lo Demás on the east were occupied by Cemetery B and El Cumbe. From her analysis of the grave wares excavated by Uhle, Menzel (1966:80) places Cemetery B within her Chincha style, prior to the arrival of the Inka in Chincha. However, this style apparently remained in use during the Late Horizon (*see* Chapters 7, 8, and 11). Use of Cemetery B as a burial ground thus may predate the occupation of Lo Demás, but by a few years at most; even if no longer in active use, the cemetery probably retained its status as a place of the dead throughout the late pre-Hispanic period. In any case, the cemetery could not have been used for agricultural purposes prior to 1901, given the good preservation of textiles (O'Neale et al., 1949; Garaventa, 1979) and other organic materials (Kroeber and Strong, 1924) in the graves excavated there by Uhle.

The shoreline at the time Lo Demás was occupied lay somewhat closer to the site than at present. Alan Craig (personal communication, 1983) sees evidence for a 1 m uplift of the Chincha coast in post-Columbian times; such an uplift would have resulted in a westward displacement of the beach. Emerged Holocene beaches are known from many points along the Peruvian coast (*see* Pozorski and Pozorski, 1979*a*:337–341; Sandweiss et al., 1983; cf. section by Hsu in Sandweiss et al., 1990); one of the best examples is the fossil lagoon at Otuma, only 50 km south of Lo Demás on the Paracas Peninsula (Craig and Psuty, 1971). Pachas T. (1983:106) mentions nine major earthquakes felt in Chincha between 1664 and 1974, and her list may not be exhaustive. However, even without recent tectonic uplift, net progradation of the coast through sedimentary processes has occurred. Pachas T. (1983: 40) mentions the "arenamiento" (sedimentation) of the old dock that was built towards the end of the last century; this dock eventually had to be abandoned because of the sand deposition. Cánepa L. (1982:88) is somewhat more explicit. He states that sedimentation of the Tambo de Mora dock began towards the end of the last century with a change in the river mouth and continued until the dock was left dry. Coker, who surveyed the Peruvian fishing industry from Paracas to Paita in 1907, has the definitive version: ". . . and even when there is a 200 m long steel dock, this is entirely dry as a consequence of the materials which the river brought down in 1904" (Coker, 1908–VI:89). The present dock, which is made of cement, also suffers from sedimentation; this dock may be the second built since Coker's visit.

The organic remains excavated at Lo Demás indicate a climate and suite of habitats similar to those found in the area today, although the distribution of habitats appears to have changed through time. With one exception, all of the mollusks found in the site are indigenous to the cold waters of the Peruvian coast; the few fragments of warm water *Spondylus* shell were almost certainly imported from Ecuador. Although it is a cool water, Peruvian bivalve, the purple mussel *Choromytilus chorus* may have been imported from south of Chincha (perhaps as close as the Paracas peninsula). The frequency of rocky shore mollusks varied throughout the archaeological sequence at Lo Demás, suggesting changes in the littoral habitats near the site during its occupation (*see* Chapter 9).

The fish species identified from the remains are all found in the Pisco–Chincha area today, as are the identified birds. The few terrestrial animals and the sea mammals are also indigenous to central Peru. However, the marine mammals were probably not available locally, but instead must have been hunted or obtained from the rocky headlands found to the south at Paracas, to the north in Cañete, or on the Chincha or Ballestas islands (*see* Fig. 1 and Chapter 9).

The crustaceans from the site, mainly the violet crab *Platyxanthus orbignyi,* are common on the Chincha shoreline today. Isotopic analysis of chitin from the carapaces of the Lo Demás *Platyxanthus* suggests a normal marine environment similar to the modern one (Schimmelmann, personal communication, 1984; Schimmelmann et al., 1986:562) (*see* Chapter 9).

Nearly all of the plant species identified from Lo Demás still grow in the vicinity of the site, although as mentioned above, there is some evidence that the distribution of fields and marshes has changed since the abandonment of the site.

Archaeological Sectors of Lo Demás

Lo Demás was initially divided into four sectors from south to north, based on the nature of the archaeological remains visible on the surface and in the eastern quebrada profile (Fig. 4). Sector I covers the southern 100 m of the site and consists of primary midden, floors, cobble and mud mortar walls, and fallen *quincha* (cane and mud) walls. The simple structures and relatively impoverished domestic midden indicate that this sector was an area of common fishermen's residences dating to the Late Horizon. Despite a few small looters' pits, the surface of Sector I shows a near-total lack of archaeological materials. Midden, floors, and walls are visible to the east in a section of quebrada-cut profile (*see* Fig. 11). In Sector I, the archaeological deposits begin within a centimeter of the modern surface.

Sector II–III covers the middle portion of the site and, despite initial separation based on preliminary inspection, is now considered as a single unit. This sector is characterized by late pre-Hispanic and possibly Initial Colonial burials intruded into cobble and *tapia* structures of late Early Horizon date (ca. 400–200 B.C., Paracas 9 affiliation: S. Massey, personal communication, 1986). The Paracas 9 structures are not visible on the surface. However, a rise on the west side of Lo Demás, just north of the border between Sectors I and II (Fig. 4), is an artificial mound with several courses of cobbles eroding out of the side. This buried mound is probably part of the late Paracas settlement.

The surface of Sector II–III is covered with visible looters' pits, while excavation revealed that other such pits had been completely filled with windblown sand. Some of the sand-filled pits were still visible in 1942 (*see* Fig. 3). Scatters of human bones, potsherds, canes, textiles, and occasionally other artifacts are found around the more recently looted burials. Debris from earlier looting has been covered by sand or destroyed by salt.

Sector IV is a zone of monumental structures and associated midden dating to the late pre-Hispanic periods and probably contemporary with Sector I. A small mound (Building IV–1) and part of a large rectangular enclosure (Building IV–2) are still preserved in this sector. The eastern two-thirds of Building IV–2 has been eroded by the quebrada during the last 40 years, leaving a long, exposed profile in which the sequence of construction of this unit is clearly visible (*see* Fig. 19). As mentioned earlier, the 1942 aerial photograph (Fig. 3) shows the zone of monumental structures continuing north for at least 250 m beyond the present limit of the site. Now completely obliterated, this extension of Sector IV included an immense platform and two large, multi-room structures, one of which appears to have been an artificial mound several times larger than Building IV–1.

EXCAVATIONS AT LO DEMÁS: DESIGN AND HISTORY

The original plan for the excavation of Lo Demás involved digging a sample of high density/high priority areas, followed by a series of randomly located test pits to determine how well the results of the judgmental sample applied to the entire site. The high priority areas were chosen on the basis of the long, continuous profiles of Sectors I and IV strata exposed along the eastern quebrada. Due to time constraints, the complexity of the microstratigraphy, and the importance given to recording each of these microstrata, I was only able to dig the judgmental sample, beginning with a test trench in 1983 and continuing with more extensive excavations in 1984. The random testing program must be carried out during a future field season. Nevertheless, several factors mitigate the problem of small sample size and allow useful conclusions to be drawn from the available data (*see* discussion of limitations in Chapter 11).

Excavations in Sector I

Archaeological investigation of Lo Demás began in August and September of 1983 with the excavation of a small test trench in Sector I of Lo Demás. The objective at this point was to confirm the indications that components of the site dated to the appropriate late pre-Hispanic time frame and that the inhabitants were fishermen, whatever other general and/or specialized activities they may have practiced. The excavation provided confirmation on both points (Sandweiss, 1983, 1988), leading to the decision to continue work at Lo Demás the following year.

The 1983 test trench was 4 m^2 and L-shaped; its long side was parallel and close to the edge of the quebrada on the east side of the site (Fig. 5). The quebrada profile along this side of Sector I showed midden throughout, deepening opposite the test trench to a maximum depth of over 2 m just east of the 1984 excavations. The location of the 1983 trench was determined by the deposits exposed in the quebrada: floors, cobble and mud mortar walls, and midden including net fragments and fish remains. Given the time constraints of the 1983 season, the deepest section of deposits exposed in the quebrada was left for the following year.

The basic horizontal divisions of the excavations were 1 m^2 subunits, organized in the 1984 excavation into 2 m^2 units (*see* Fig. 5 for subunit designations). Within each subunit, excavation proceeded by natural levels and features (*see* Sandweiss, 1989:116–118, footnote 93 for details of level and feature designations). Each level, sublevel, feature, or subfeature in each subunit was considered a separate provenience and assigned a catalog number.

Of the four subunits in the 1983 test trench, two were excavated to sterile ground, which was encountered at a maximum depth of 0.75 m below the surface. Parts of three subunits (A1, A3, B3) were left unexcavated or partially excavated (*see* Table 1). All excavated materials were screened with 0.25-in mesh, and in some cases the material that passed through the screen was saved for future analysis.

In 1984, excavations in Sector I were located from 0.75 and 2.00 m south of the 1983 test trench, above the deepest deposits revealed in the quebrada profile. Eighteen subunits pertaining to five units were opened (Fig. 5); 14 were wholly or partially excavated to sterile ground (*see* Table 1), which was encountered at a maximum depth of 1.30 m below the surface. A 0.20 m^2 column was left standing in the four corners of each 2 m^2 unit (Fig. 5). At the end of the season, a 0.40 m^2 column (combining the adjacent columns of subunits 2A, 4B, 10D, and 1C) was removed by natural levels without screening.[43] In addition, an unscreened sample from which the artifacts had been removed was kept from each provenience (subunit/level or subunit/feature). These samples measured about 400 cm^3. In the case of very small proveniences (under ca. 800 cm^3), the artifacts were removed and the entire unit was saved without screening. The rest of the excavated material was passed through 0.25-in screen.

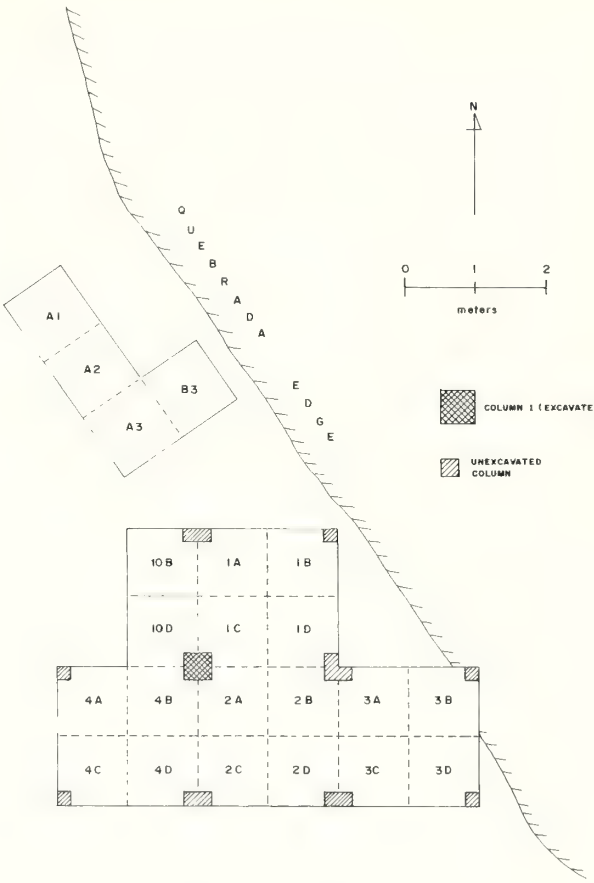

Fig. 5.—Configuration of the 1983 and 1984 excavations in Sector I of Lo Demás. See Fig. 4 for location of the excavations within the site as a whole.

Excavations in Sector II–III

Excavations were opened in Sector II in 1984 to find burials associated with the fishing settlement at

Lo Demás. The area selected (*see* Fig. 4) appeared to be the least affected by looting. The results of the excavation were surprising. First, despite the level appearance of the surface, the area is peppered with looters' holes. Second, walls and floors of a different construction from those in Sector I underlie the entire area. As discovered later, these features are part of structures that date to late in the Early Horizon (Paracas 9), over 1,500 years prior to the late pre-Hispanic fishing occupation at Lo Demás. Finally, although there were late pre-Hispanic (and/or Initial Colonial) burials present in the area, the lack of contemporary, late pre-Hispanic residential deposits and the scarcity of diagnostic grave goods made it impossible to relate these burials directly to the fishing occupation of the site.

Because of these dating and correlating difficulties, excavations in Sector II–III will be discussed peripherally.

Excavations in Sector IV

In Sector IV, two excavations were carried out: Room IV–1a in Building IV–1 was cleared and Subunit 26D was excavated adjacent to Building IV–2 (Figs. 4, 6). Room IV–1a was cleared after the discovery of mural paintings on the two surviving walls of the chamber (*see* Chapter 6). Erosion of Building IV–1 by the quebrada had removed the north and east walls of the room, and the material with which it had been filled during a later construction phase was slowly disappearing into the quebrada while revealing the paintings. After excavation of the remaining fill to the surface of the floor associated with the room, Peruvian National Institute of Culture conservator E. Guzmán stabilized the murals in accordance with Institute practice.

Table 1.—*Depth of excavation in subunits from Sector I, Lo Demás.*

Year	Subunit	Excavated to
1983	A1	Top of Complex A
	A2	Sterile
	A3	Top of Complex A
	B3	Sterile
1984	1A	Sterile
	1B	Within Complex C
	1C	Sterile
	1D	Within Complex C
	2A	Sterile
	2B	Sterile
	2C	Sterile
	2D	Sterile
	3A	Sterile
	3B	Sterile
	3C	Sterile
	3D	Sterile
	4A	Top of Complex C
	4B	Sterile
	4C	Top of Complex C
	4D	Sterile
	10A	Not excavated
	10B	Sterile
	10C	Not excavated
	10D	Sterile

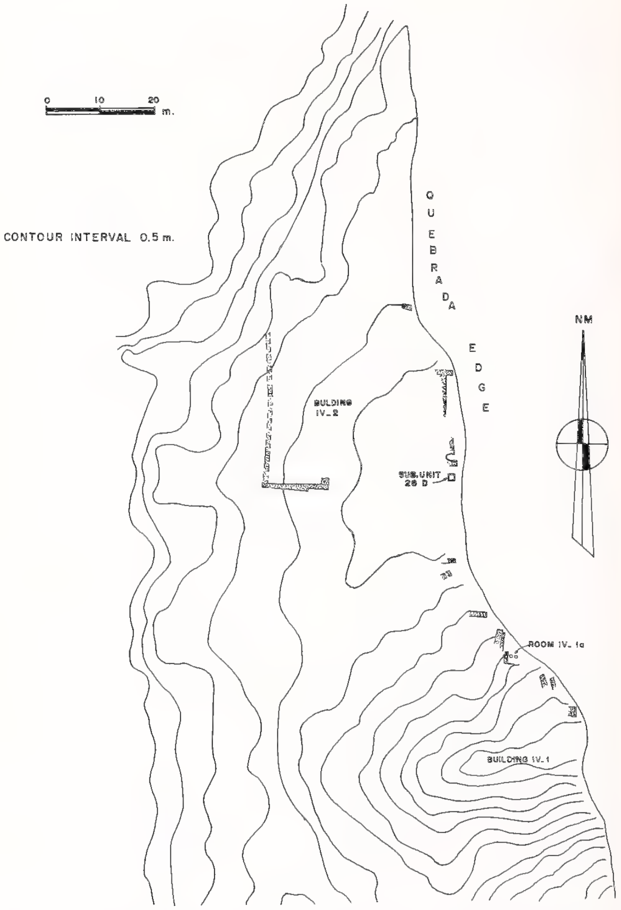

Fig. 6.—Detail of Sector IV of Lo Demás, showing the location of Subunit 26D and Room 1a. Fig. 4 shows the position of Sector IV within the site as a whole.

Immediately adjacent to the south side of Building IV–2, the quebrada profile showed the majority of the strata dipping south, apparently having been thrown or fallen from this building during its use (Fig. 7). I placed Subunit 26D in this area, 1.9 m south of Building IV–2 and 0.30 m west of the quebrada edge, on the assumption that the deposits there would reflect the activities carried out in Building IV–2.

The excavation of Subunit 26D followed the same methodology as described for the 1984 excavations

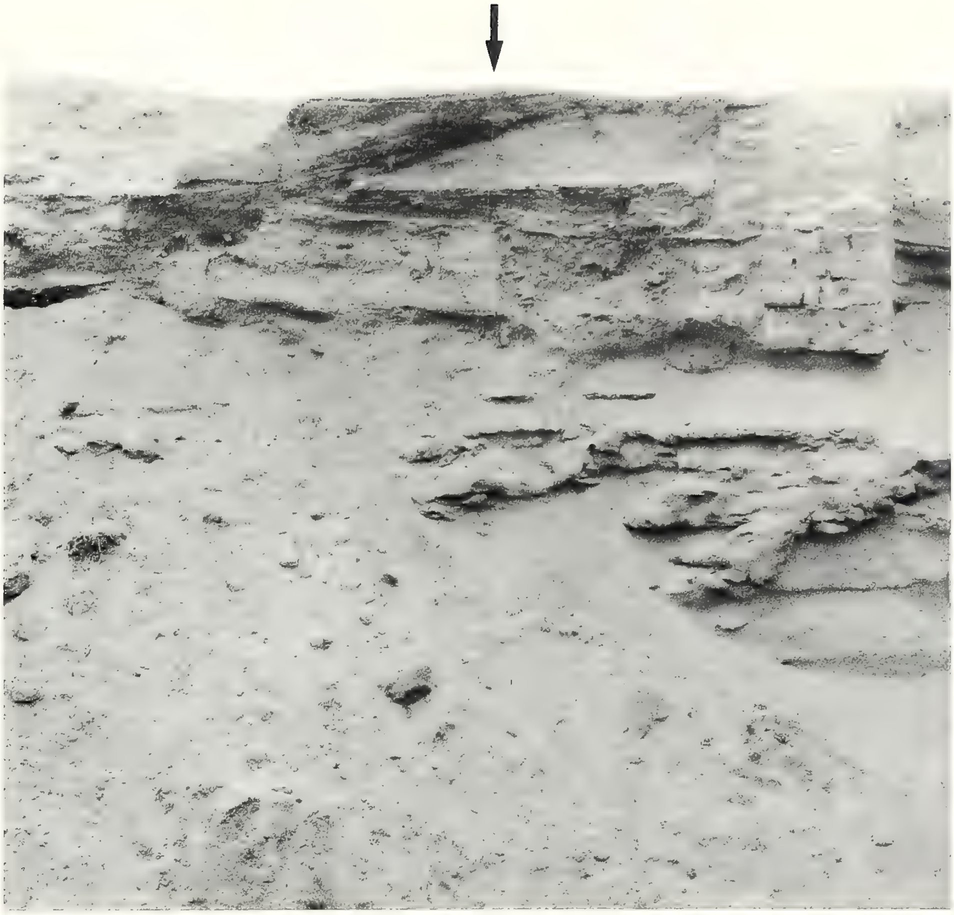

Fig. 7.—Quebrada profile adjacent to Subunit 26D. Subunit 26D is located just behind and to the left of the vertical cord (below arrow) in the center of the photograph. View is west to east.

in Sector I. A 0.20 m^2 column was left intact in the southeast corner of the subunit and was later removed without screening (*see* note 43). Excavation stopped at a floor that forms part of the major construction phase of Building IV–2 defined in the quebrada profile, at a maximum depth of 1.35 m below the surface.

Excavations at Lo Demás: Stratigraphy

Sector I

Although 1,306 proveniences were excavated in Sector I, all of the levels and features could be grouped during analysis into four stratigraphic complexes (*see* Figs. 8, 9 and Sandweiss, 1989:Appendix

B). Each complex is designated by a letter and a descriptive label, from the lowest (A) to the highest (D). The stratigraphic complexes cover both the 1983 and the 1984 excavations (Table 2).

A. Basal Complex.—This complex underlies the Sector I deposits and conformably covers the original topography, which is composed of the easily recognized, alternating sand and clay layers of the Topará Formation. Of variable thickness (2 to 30 cm), Complex A has almost no archaeological material; the few remains are probably intrusive from the overlying levels. At the very least, the material is scarce enough to suggest that this complex represents an ephemeral human presence at the site, not local habitation. No radiocarbon dates are available for this complex.

B. Lower Complex.—The Lower Complex consists of east- and northeast-dipping strata of primary, generally high density midden, and it provides the first clear evidence of human habitation in Sector I. The eastward slope of this complex conforms to the original topography, which drops sharply to the east into the quebrada. The lack of walls, hearths, or constructed or use-trampled floors in the Lower Complex, together with the eastward slope, imply that the complex was deposited from a habitation focus to the west of the excavation area. This complex was not present in the 1983 test trench, probably because the midden was being thrown into what appears to have been a channel or gully in the side of the quebrada underlying the 1984 excavation area. The base of the Unit 3 north profile (Fig. 9) shows the former quebrada edge as revealed under the excavations in Sector I. Deliberately or not, the first inhabitants of this sector practiced a kind of land fill. Marcus (1987*a*:398) reports a somewhat similar pattern of gully filling and terrace construction at Cerro Azul, a Late Intermediate Period fishing site in the neighboring Cañete valley.

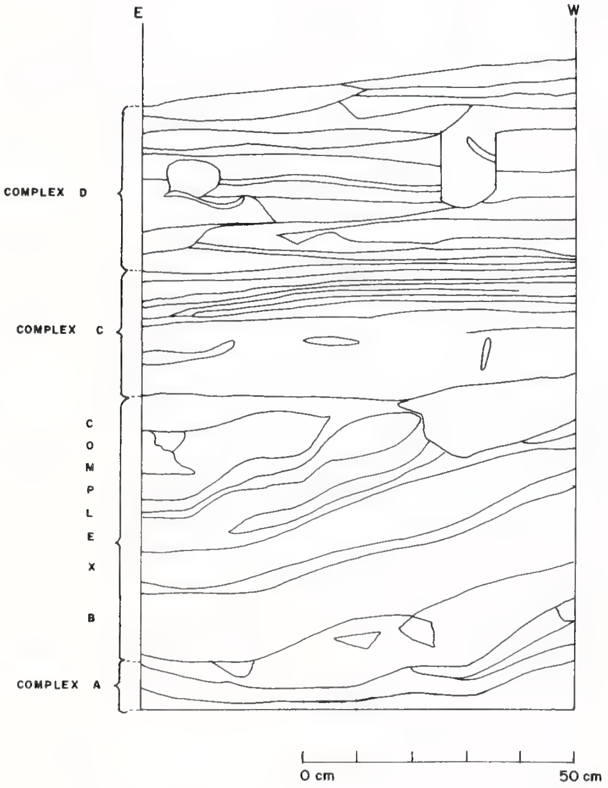

Fig. 8.—South profile of Subunit 2C from the 1984 excavations in Sector I of Lo Demás, showing Stratigraphic Complexes A, B, C, and D.

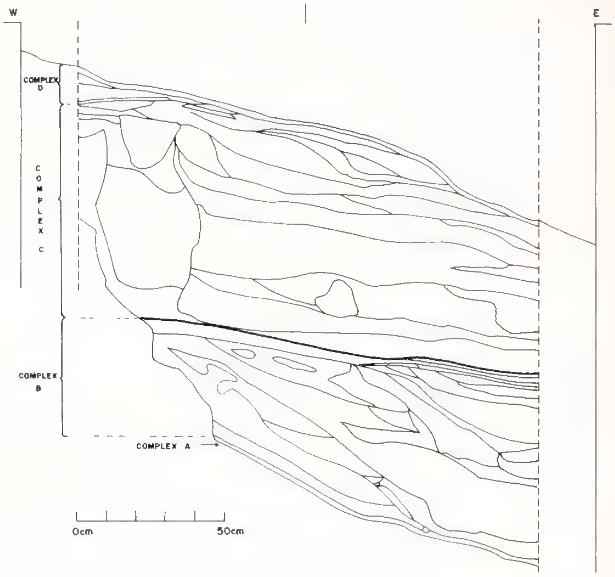

Fig. 9.—North profile of Subunits 3A and 3B from the 1984 excavations in Sector I of Lo Demás, showing Stratigraphic Complexes A, B, C, and D.

Four radiocarbon dates are available for the Lower Complex (Table 3, Fig. 60). One date (260 ± 100: A.D. 1690 [BGS 1195]) is inconsistent with the other three Lo Demás dates, and is discounted as anomalous.[44] The other dates have an average uncorrected mean of 433: A.D. 1527, or an average calibrated (Stuiver and Pearson, 1986) mean of A.D. 1460.

C. Middle Complex.—This complex represents the earliest habitation of the *excavation area* in Sector I, though the earliest occupation of the *sector* was during the Lower Complex. At the beginning of the

Table 2.—*Correspondence of the stratigraphic complexes defined for Sector I with the levels reported in Sandweiss (1988) from the 1983 test trench.*

	Stratigraphic Complex	Original Level Designation in 1983 Test Trench (Sandweiss, 1988)
Top	Mixed surface deposits	Level 1
	D. Upper Complex	Level 2
	C. Middle Complex	Level 3
	B. Lower Complex	Not present
	A. Basal Complex	Level 4
Bottom	Sterile	Sterile

deposition of the Middle Complex, the inhabitants of Lo Demás levelled the Lower Complex deposits and began to live in the excavation area. The process of levelling the older, east-dipping strata is clearest in Unit 3, where the Middle Complex begins with a clay floor constructed over truncated Lower Complex strata and associated with a clay wall (*see* Fig. 9 and Chapter 6).

The Middle Complex consists of horizontal floors (both constructed and use-trampled) and midden levels, punctuated by pits, postholes, channels, and hearths (*see* Chapter 6). Its stratigraphically highest level is a clay floor that was present in all of the excavated subunits, and which underlay the cobble and mortar walls of the next complex (D). The Middle Complex was found superimposed directly on the Basal Complex in the 1983 test trench (*see* Table 2).

The single radiocarbon date for the Middle Complex is 400 ± 130: A.D. 1550 (uncorrected, BGS 1192), or A.D. 1480 (calibrated, Stuiver and Pearson, 1986) (*see* Table 3 and Fig. 60).

D. Upper Complex.—The Upper Complex is the final occupation level in Sector I of Lo Demás; it began with the construction of cobble and mud mortar walls and an associated clay floor. Above this floor, which was poorly defined in some subunits, this complex is composed of use-trampled floors and midden deposits broken by pits, postholes, hearths, and channels (*see* Chapter 6). The accumulation of the Upper Complex is thus similar to that of the Middle Complex, with two exceptions. First, unlike the wall in Unit 3 in the Middle Complex, the cobble walls apparently represent a building phase that extended over much of Sector I (*see* Chapter 6). Second, the upper part of the Upper Complex in Unit 4 contains evidence of a curved *quincha* structure possibly related to cane-filled channels in Units 1 and 2 (*see* Chapter 6). The intervention of the cobble and mud mortar wall prevents exact correlation between the levels in the eastern and western half of the Upper Complex.

Table 3.—*Radiocarbon dates from Lo Demás. Abbreviations: SC, stratigraphic complex (applicable only to Sector I proveniences); Cat., catalogue number (Sandweiss, 1989:Appendix B). The "Date" column shows the uncorrected dates. The "Calibrated" column is based on the graphs published by Stuiver and Pearson (1986), using the 30-year southern hemisphere reduction (Stuiver and Pearson, 1986:809). In this column, the range of dates represents one standard deviation around the mean (not always symmetrical). In some cases, the graphs yield multiple dates (all spans are reported, but only the most likely mean).*

Sample	Subunit	Cat.	SC	Date	Calibrated
BGS 1191	1C	478	D	350 ± 80 A.D. 1600	A.D. 1460–1654 A.D. 1523
BGS 1192	10B	789	C	400 ± 130 A.D. 1550	A.D. 1420–1650 A.D. 1480
BGS 1195	3B	1535	B	260 ± 100 A.D. 1690	A.D. 1400–1680 A.D. 1660
BGS 1197	4B	1856	B	400 ± 100 A.D. 1550	A.D. 1380–1580 or 1430–1650 A.D. 1480
BGS 1198	4D	1857	B	450 ± 80 A.D. 1500	A.D. 1422–1514 or 1599–1616 A.D. 1448
BGS 1194	1C	1201	B	450 ± 80 A.D. 1500	A.D. 1422–1514 or 1599–1616 A.D. 1448
BGS 1196	26D	1718	—	475 ± 140 A.D. 1475	A.D. 1300–1585 or 1390–1640 A.D. 1440
BGS 1199	26D	1874	—	380 ± 90 A.D. 1570	A.D. 1415–1595 or 1445–1650 A.D. 1500

The one radiocarbon date for the Upper Complex, the youngest from Sector I (except for the anomalous Complex B date) is 350 ± 80: A.D. 1600 (BGS 1191, uncorrected), or A.D. 1523 (calibrated; *see* Table 3 and Fig. 60).

Above the Upper Complex, a thin layer of loose surface debris averaging about 1 cm in thickness covered the archaeological levels and contained abundant feces of sheep and goats, along with other occasional items of post-Hispanic origin. This layer is not included in the stratigraphic complexes.

Sector IV

Two excavations were carried out in this sector, in Room IV–1a and in Subunit 26D. The stratigraphy of Room IV–1a has little significance; although four levels were distinguished, all consisted

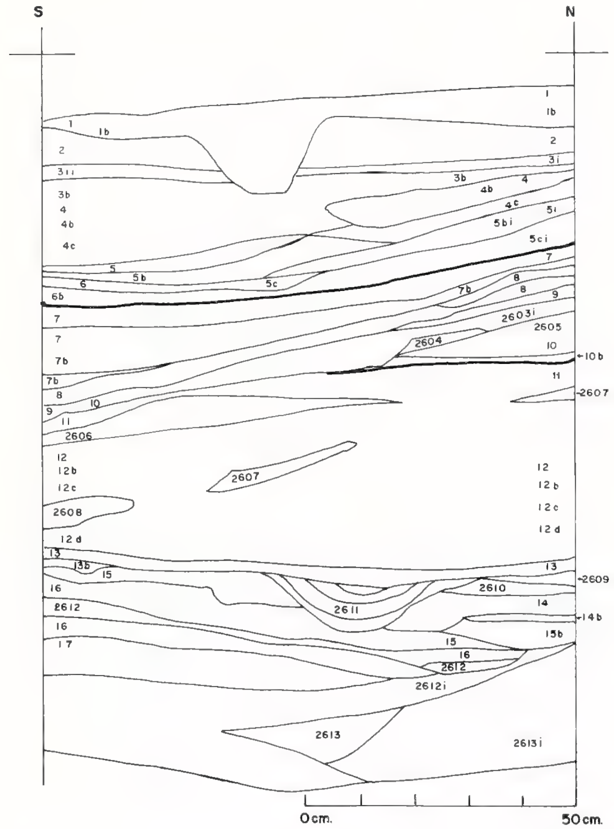

Fig. 10.—West profile of Subunit 26D in Sector IV of Lo Demás, showing features (four-digit numbers beginning with "26") and levels.

of fairly homogeneous fill that was probably deposited during a single building phase in Building IV–1, subsequent to the construction and use of Room IV–1a (*see* Chapter 6). Unlike the rest of the excavations at Lo Demás, I excavated Room IV–1a (of which less than 3 m^2 of floor area were preserved) as a single unit, not subdivided into 1 × 1 m subunits.

Due to the small size of Subunit 26D, major stratigraphic groupings could not be distinguished. From the adjacent quebrada profile, however, it is clear that the base of the excavation rests on a constructed floor related to the major building phase of Building IV–2 (*see* Chapter 6). As mentioned earlier, the strata in Subunit 26D tend to dip to the south, away from Building IV–2 (Fig. 10). The levels consist of floors, midden deposits, and wall fall. Compared with the Sector I subunits, Subunit 26D has fewer features such as pits or postholes.

The two radiocarbon dates available for Subunit 26D (*see* Table 3 and Fig. 60) do not fit stratigraphic order, suggesting that the upper levels of this subunit may be mixed with earlier material (*see* Chapter 9, section on shells). The older date, from level 26–3b, is 475 ± 140: A.D. 1475 (uncorrected, BGS 1196). The younger date, from level 26–17, is 380 ± 90: A.D. 1570 (uncorrected, BGS 1199). The calibrated mean dates for these two assays are A.D. 1440 and A.D. 1500, respectively. The range of these dates is consistent with the Sector I dates, indicating contemporaneity between the two sectors.

Conclusions

Excavations in Sector I of Lo Demás defined four stratigraphic complexes, A to D, each representing a different depositional activity in the excavated area. These complexes form the basic units for the analyses of the Sector I materials. In Sector IV, the deposits from Subunit 26D pertain to one phase in the construction sequence of Building IV–2 and therefore are treated as a single analytic unit.

Deposits of clean, windblown sand were almost completely lacking within or between the Sector I complexes or between the Subunit 26D levels; the few small occurrences had no lateral extension. Given our experience with the effect of seasonal "paracas" winds and the presence of standing architecture during most of the occupation, this fact suggests that the habitation of the site was continuous from the beginning of the Lower Complex to the end of the Upper Complex. The only unconformity occurs between the Lower and Middle Complexes; this break is well defined only in Unit 3, where it is clearly the result of construction activity by the site's inhabitants. In the other units, the Middle Complex seems to lie more conformably on the Lower Complex.

CHAPTER 6

ARCHITECTURE AND FEATURES: SECTORS I AND IV

This chapter covers only those architectural and archaeological features[45] that are significant for identifying activities carried out at Lo Demás or for relating the site's inhabitants to other occupants of the Chincha valley.

Sector I

Examination of the surface and the exposed, eastern quebrada profile of Sector I reveals one major architectural element: low, cobble-and-mud-mortar walls. Standing walls are visible in the profile (*see* Fig. 11), whereas on the surface, only scattered cobbles can be seen. However, the surface outcrops do occasionally appear as small, aligned groups of cobbles set in mortar.

During the excavations in 1983 and 1984, the cobble and mud mortar walls were associated with the latest occupation of Sector I (Stratigraphic Complex D, Chapter 5). In the 1984 excavation area, a clay floor was built between the two north–south walls, and another floor was associated with the base of the east–west wall in the 1983 test trench. Fig. 12 shows the plan of the Complex D walls in both excavation areas and the probable connection between the two areas. The cobble walls apparently formed large, more or less rectangular rooms; one such room (Room I–1) lay between the north–south walls in the 1984 excavation area, and others were probably located to the east of the central wall (Room I–2) and to the north of the east–west wall in the 1983 excavation area (Room I–3).

In the 1984 excavations, *quincha* structures were found within the Upper Complex (D) but stratigraphically higher than the construction of the walls (Sandweiss, 1989:146, Fig. 19). Unit 4 contained a semicircular channel with a number of in situ, upright cane bases, and a hearth in association with the earliest floor of the semicircular *quincha* structure. Underneath this floor were two small, circular pits (5 cm diameter, 1 to 2 cm deep) filled with burnt fish, possibly offerings deposited in association with the construction of the *quincha* structure. Another, later hearth also apparently associated with this structure was found between Units 1 and 2. Straight channels, often with pieces of canes still in vertical position, were excavated in Units 1 and 2. All of the channels are higher stratigraphically than the cobble walls, showing that the *quincha* structures are part of Complex D.

Underlying the *quincha* structure in Unit 4, but still above the base floor of Complex D, was another large hearth (approximately 130 cm × 50 cm). Several other hearths were found in Complex D, including an ash zone next to an ash-stained segment of the wall in Subunit 2C. All of these hearths are in Room I–1, on the west side of the central cobble wall, and each is associated with a different sublevel of Complex D, which may indicate that Room I–1 was a locus of domestic activity throughout Complex D. However, the distribution of hearths may be biased by preservation and sampling. Because of erosion by the quebrada, Room I–1 covered slightly over twice as much area as Room I–2. Another Complex D hearth was located in Room I–3, Subunits A2 and A3, suggesting a second domestic locus in that room.

Thirty-nine pits were found during the excavation of Stratigraphic Complex D. Horizontal dimensions range from over 50 cm to under 5 cm, and depths range from a few centimeters to as much as 30 cm. Some of the pits were probably holes for roof posts, while others most likely served for household storage. The form of one of the pits at the base of Complex D in Unit 3[46] suggests that it may have served as a jar rest for a conical-based pot (Sandweiss, 1989: 149, Fig. 20). A conical base from a large storage jar excavated from Subunit 26D in Sector IV (Sandweiss, 1989:150, Fig. 21) and several similar bases from the quebrada near Sector IV show that such pottery was in use in the area.

Cobble and mud mortar walls are not present in Stratigraphic Complex C, the Middle Complex. Prepared and use-trampled floors are a defining element of this complex, but only one wall was found, made of up-ended slabs of the geological strata underlying the site (though the wall may have been made by mixing local sand with mud mortar to make a cement resembling these strata). The Middle Complex wall lies in Subunits 3A and 3C, with a slight extension into 2B, and runs approximately NNW–SSE. When first constructed, in association with a prepared clay bench and floor that overlies truncated midden strata of the Lower Complex, there may have been a narrow entrance in the middle of

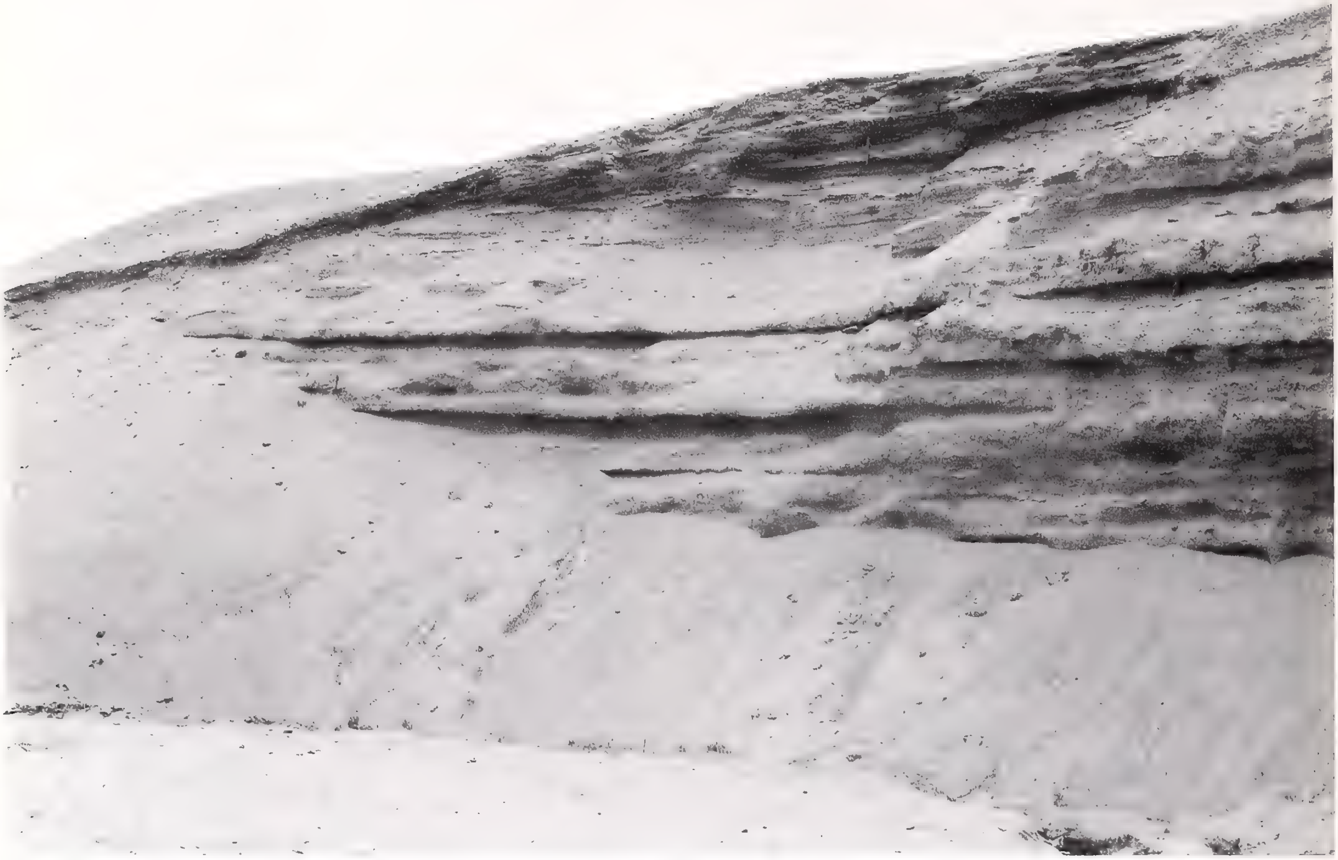

Fig. 11.—Quebrada profile on the east side of Sector I, view is NE to SW; note continuous archaeological deposits along top of quebrada. The Sector I excavations (Fig. 5) were located just west of the cobble and mud mortar walls in center top.

the wall. Capping the wall and dating to late within the Middle Complex is a wide clay platform topped with a single line of small cobbles.

A number of channels were found in Complex C, but they tend to be wider than those in Complex D. In the 1983 excavation area, a series of four parallel channels in two sets connect a number of circular pits (Fig. 13). Each set of two channels runs about 25 cm apart, whereas the two sets are separated by about 50 cm. Abundant fish remains occurred in the channels (*see* Chapter 9). These features may be the remains of drying racks for salted fish (Sandweiss, 1983, 1988); they closely resemble the plan of a traditional fish salting and drying workshop in Tambo de Mora (Fig. 14). In the modern workshop, lines of posts supporting the racks run in parallel groups of two with the members of each group close together; the groups are more widely separated. This arrangement allows maximum utilization of available space: workers can walk in the wider spaces between each set of racks, hanging fish both left and right. The channels connecting the postholes could have resulted from water dripping off of the fish as they dried.

Two features from different parts of Complex C also appear to have been involved in fish salting and drying. Located in Subunits 4D and 10B, these features consist of plant fiber mats associated with fish remains and small lumps of salt. Fiedler et al. (1943: 78–79) describe a method of salting *anchovetas* (the most common species of fish excavated from Lo Demás, *see* Chapter 9) by placing them on reed mats, throwing "salitre" (a naturally occurring mix of salt, sand, and other minerals) on the fish, and leaving them in the sun to dry. This technique would leave remains similar to the two features under consideration (*see* Fiedler et al., 1943:79).

As in the Upper Complex, pits of varying size are

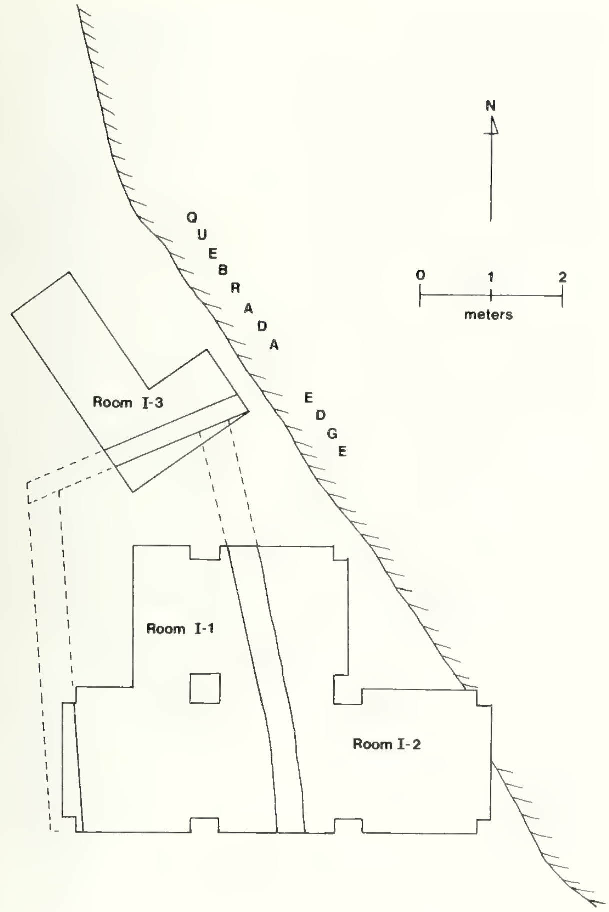

Fig. 12.—Plan of Complex D walls in the 1983 test trench and in the 1984 excavations in Sector I of Lo Demás, showing Rooms I–1, I–2, and I–3. The black-outlined, rectangular areas are the excavation units (*see* Fig. 5 for the layout and numbering of units and subunits). Solid, parallel black lines within the units are walls; dashed lines are projected walls.

common in the Middle Complex. Some were probably postholes. The pits associated with the possible fish-drying racks have already been mentioned. Dead animals were placed in a number of holes (*see* Chapter 9). In Subunit B3, an entire, grey-headed albatross (*Diomedea chrysostoma*) had been deliberately interred (Fig. 15); another bird was buried in a pit beneath the later wall in the same unit but was left in situ because the wall was not removed. These birds were most likely offerings. Two intact guinea pigs were found in separate pits in Complex C; two others from this complex were encountered together in a midden stratum. Although the guinea pigs (especially those in the pits) may have been offerings, their condition strongly suggests that they were first involved in a curing ritual (*see* Chapters 9, 11). A fish head found in a small hole to the side of a large pit in Subunit 3C also appears to have been buried deliberately.

In Subunit 2D, a circular pit (26 cm diameter) contained a large fragment of red, oxidized pottery and abundant salt and food remains. This pit may have served as a jar rest for the pot represented by the sherd. Another shallow, circular pit in Subunits 1C and 10B contained a variety of small objects that suggest an offering, including: a piece of plant fiber (possibly a maize leaf) torn into strips and braided into a netlike form; a leg and part of a head from a figurine (Fig. 34); and a number of small, hard clay balls, averaging a little under one cm in diameter.

Only one hearth was uncovered in Complex C, in Subunits 1C, 2A, and 2B (it extended into the unexcavated portion of 1D). The hearth was larger and better defined than any of those in Complex D, and indicates that the area excavated in 1984 was

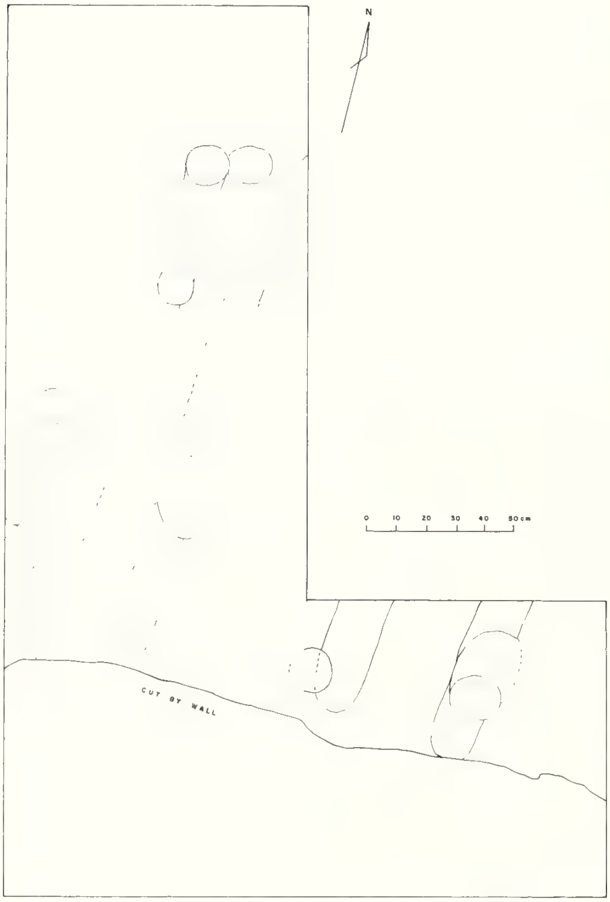

Fig. 13.—Plan of parallel channels and pits in 1983 Subunits A1, A2, A3, and B3, Sector I of Lo Demás (*see* Fig. 5). These features may be the remains of fish-drying racks.

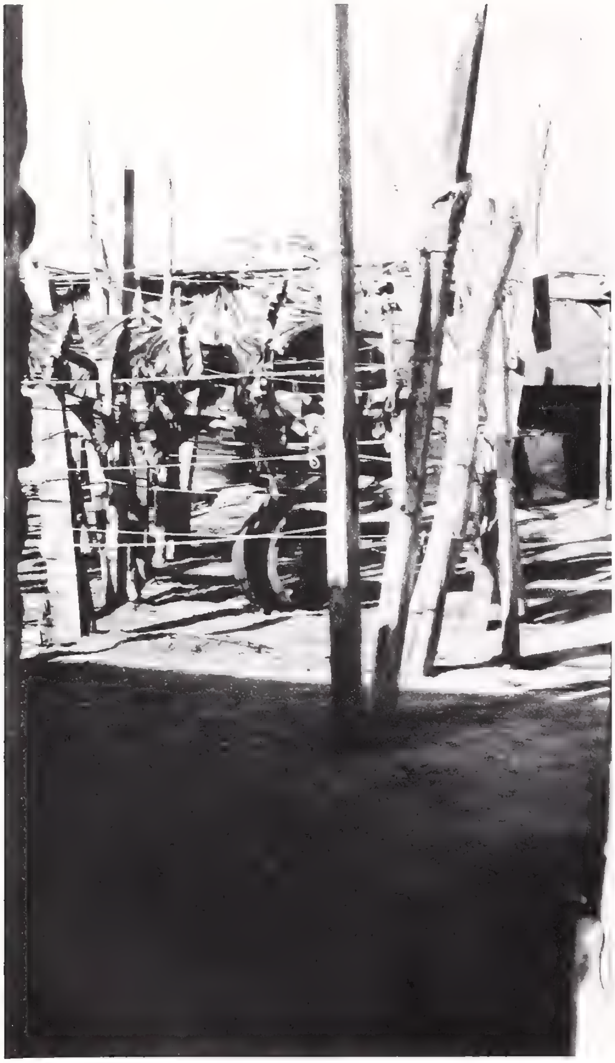

Fig. 14.—Traditional fish salting and drying workshop in Tambo de Mora, Chincha, Peru. Note the double rows of posts separated by wider walkways.

a locus of domestic activity during the deposition of Complex C, a conclusion supported by the multiple floors. The area excavated in 1983, however, appears to have been a fish drying workshop at this time (*see above*).

As noted in Chapter 5, Complex B is interpreted as a set of midden strata deposited from a locus of domestic activity to the west of the excavation area. Consistent with this interpretation, Complex B has very few pit features and no architectural features. The scarcity of pits is particularly striking in contrast to the large number of such features in the two later complexes (C and D). One intact guinea pig was found in Complex B at the interface with the underlying Basal Complex. Also at this interface was an accumulation of burnt material, including pieces of clay, which may be the remains of a small hearth. Both the possible hearth and the guinea pig could be assigned to either Complex B or Complex A.

Associated with Complex A, the Basal Complex, one intact guinea pig had been placed on the underlying sterile ground beneath a natural overhang of the former quebrada edge in Subunit 3D, unaccompanied by any other special items. Otherwise, this complex has almost no features and very few remains of any kind.

Sector IV

The extremely limited excavations in Sector IV uncovered few significant features. However, the monumental nature of the structures in this sector, combined with the information provided by the quebrada profile, allowed recording of a number of architectural details. The two surviving structures, Building IV–1 and Building IV–2, have elements of form and construction that indicate the presence of elite residents in this sector of Lo Demás.

Building IV–1 is a low, stepped mound 3 to 4 m high (Figs. 3, 4, and 6). Its eastern and northeastern faces have been eroded by the quebrada, but the mound retains much of its original form. Building IV–1 is aligned north–south (unlike the east–west alignment of stepped platforms in earlier periods in Chincha, *see* Sandweiss, 1989:74–85); there are at least three platform levels on the southern side of the mound, with the highest level to the north of the structure's center.

Only one platform level is found to the north of the summit of Building IV–1, and all that remains of this level is part of a chamber labelled Room IV–1a. Only the south wall and a section of the west wall of this room survive, along with a triangular wedge of the original floor containing two postholes (Fig. 6). Chips of wood and other debris suggesting roof fall were found on the floor. At the time Room IV–1a was used, the walls were whitewashed and painted with a series of geometric birds. One bird in black outline with red fill was on the west wall, along with black lines probably pertaining to another bird, now eroded beyond recognition (Fig. 16). The south wall had one well-preserved bird painting with net-like cross-hatching filling the body, another figure that was still recognizable as a bird, and some indecipherable lines (Fig. 17). Red fill was not used in the south wall paintings. The surviving birds all share formal characteristics: rhomboidal bodies, tri-

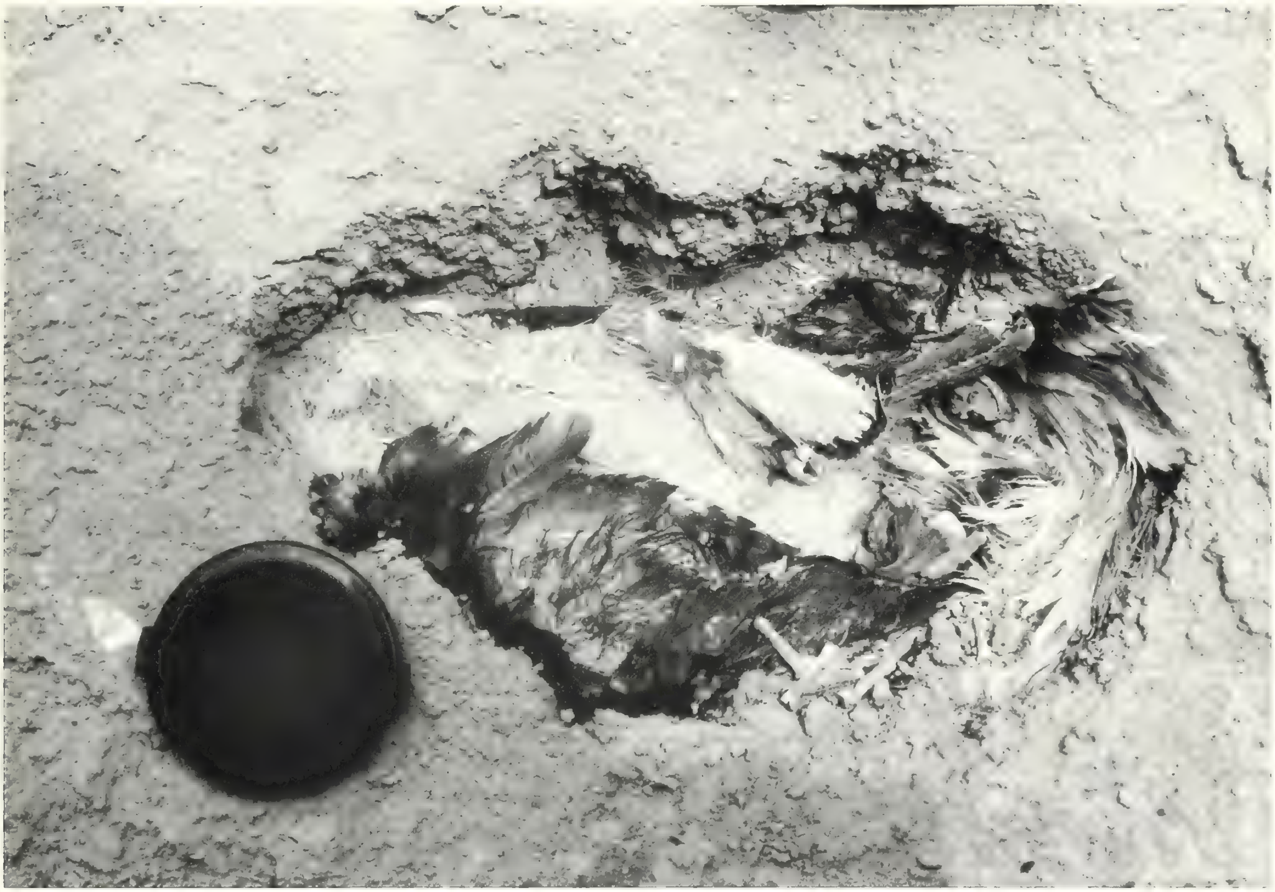

Fig. 15.—Deliberately interred grey-headed albatross (*Diomedea chrysostoma*), Complex C, Subunit B3, Sector I, Lo Demás.

angular tails, long necks, long legs, circular heads with a round dot representing the eye, large double beaks, and wings that are variations on a step motif. Several of these characteristics (long legs and neck, large beak) suggest that the paintings represent marine species.

An Ica 10 pot (Menzel, 1976:Plate 63, No. 100, immediately postconquest)[47] provides a striking parallel with Building IV–1 and Room IV–1a at Lo Demás (Fig. 18). This vessel represents a stepped structure with three levels and white walls. The upper two levels have open sides but are covered by roofs supported by two posts. Small, modeled, anthropomorphic figures are visible on these levels. The lowest level has a modeled, seated, quadruped and a row of three painted bird figures that share formal characteristics with the figures in Room IV–1a: black outlining on a white background, rhomboidal bodies, long legs, large beaks, and circular heads with dot eyes. Fishing (sea) birds appear to have been important symbols for the fishermen of Chincha (*see* Chapter 9, section on Vertebrate Remains Other Than Fish).

The conjunction between the ceramic model from Ica and Building IV–1 at Lo Demás suggests that such structures were well-known on the south coast during late pre-Hispanic times. It also supports a very late date for Building IV–1, though given the inferred revivalist nature of Ica 10 pottery (*see* note 47), the strong identity between the structure and the pot does not require an Ica 10, Early Colonial assignment to Building IV–1. Room IV–1a was deliberately filled at some point in the history of Building IV–1; pottery from the fill dates to the late Late Intermediate Period, so Room IV–1a was filled during or after that time. All of the evidence indicates a Late Horizon date for Building IV–1 and makes sense in light of the Late Horizon date for the adjacent Building IV–2. The quebrada profile reveals continuous archaeological deposits between the structures, linking them temporally. The chronological assignment of Building IV–2 is based mainly

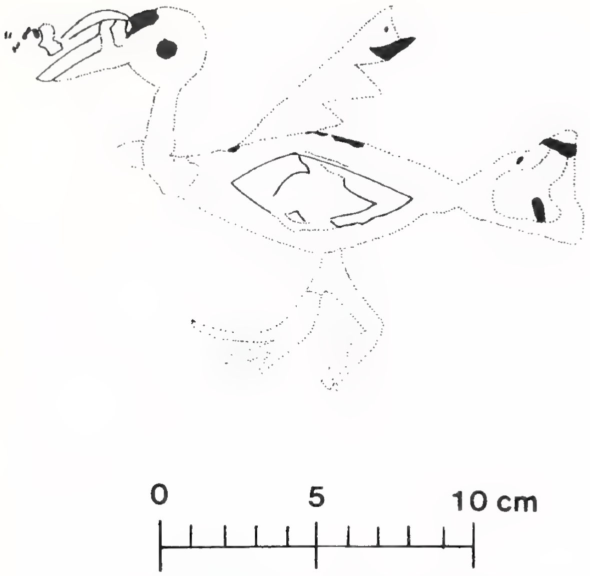

Fig. 16.—Drawing of the bird painting on the west wall of Room IV–1a in Building IV–1, Sector IV of Lo Demás. The figure is in black; faint traces of red were visible around the eye and filling the central rhomboid.

on the ceramics recovered from Subunit 26D, the radiocarbon dates, and the use of rectangular *adobes* (*see* Chapters 5, 7, 8, and 11). Whereas Building IV–1 was built of *tapia* walls with occasional cobbles and only one visible *adobe* wall, most of the major walls of Building IV–2 seen in the quebrada profile are made of large, rectangular *adobes* and only a few are of *tapia* (Fig. 19). In Chincha, large rectangular *adobes* are associated with Inka structures[48] (Santillana, 1984; Wallace, 1972; *see* Chapter 4). The construction materials used for Building IV–2 therefore support the Late Horizon date for it and, by association, for Building IV–1.

Building IV–2 underwent at least two phases of construction as revealed by the quebrada profile (Fig. 19). During the earlier phase, a number of floors and *tapia* walls were built. The southernmost rectangular *adobe* wall may have been built at this time; however, the use of rectangular *adobes* and the retaining function of the wall (Sandweiss, 1989:164, footnote 109) suggest that it was built after the *tapia* walls, at the very start of the second construction phase. During the second and major building stage, the central portion of Building IV–2 was levelled with midden fill on which clay floors and rectangular *adobe* walls were erected. Following this construction, the building gradually filled in, first from human deposition (as recorded in the strata of Subunit 26D) and late from wind-blown sand. The dating of the structures that once existed to the north of Lo Demás (*see* Chapter 5) as Late Horizon is based only upon their apparent association with the surviving buildings of Sector IV. No traces of these structures or associated materials are left.

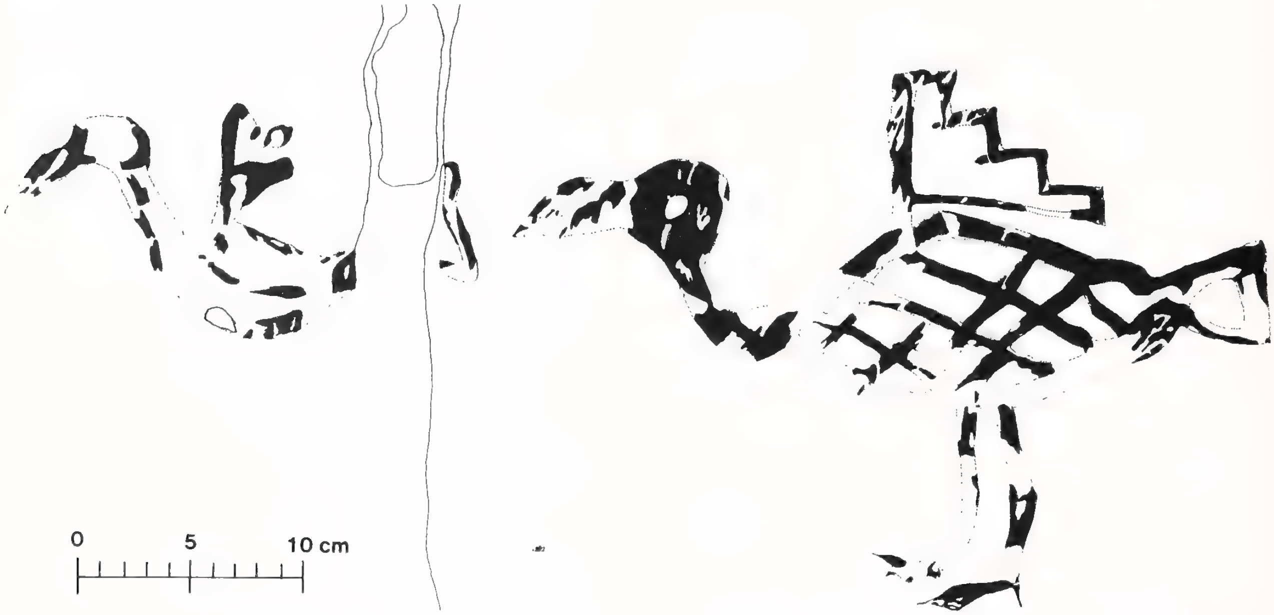

Fig. 17.—Drawing of the bird paintings on the south wall of Room I–1 in Building IV–1, Sector IV of Lo Demás. The figures are entirely in black on a whitewashed background; there were no traces of red paint on the south wall.

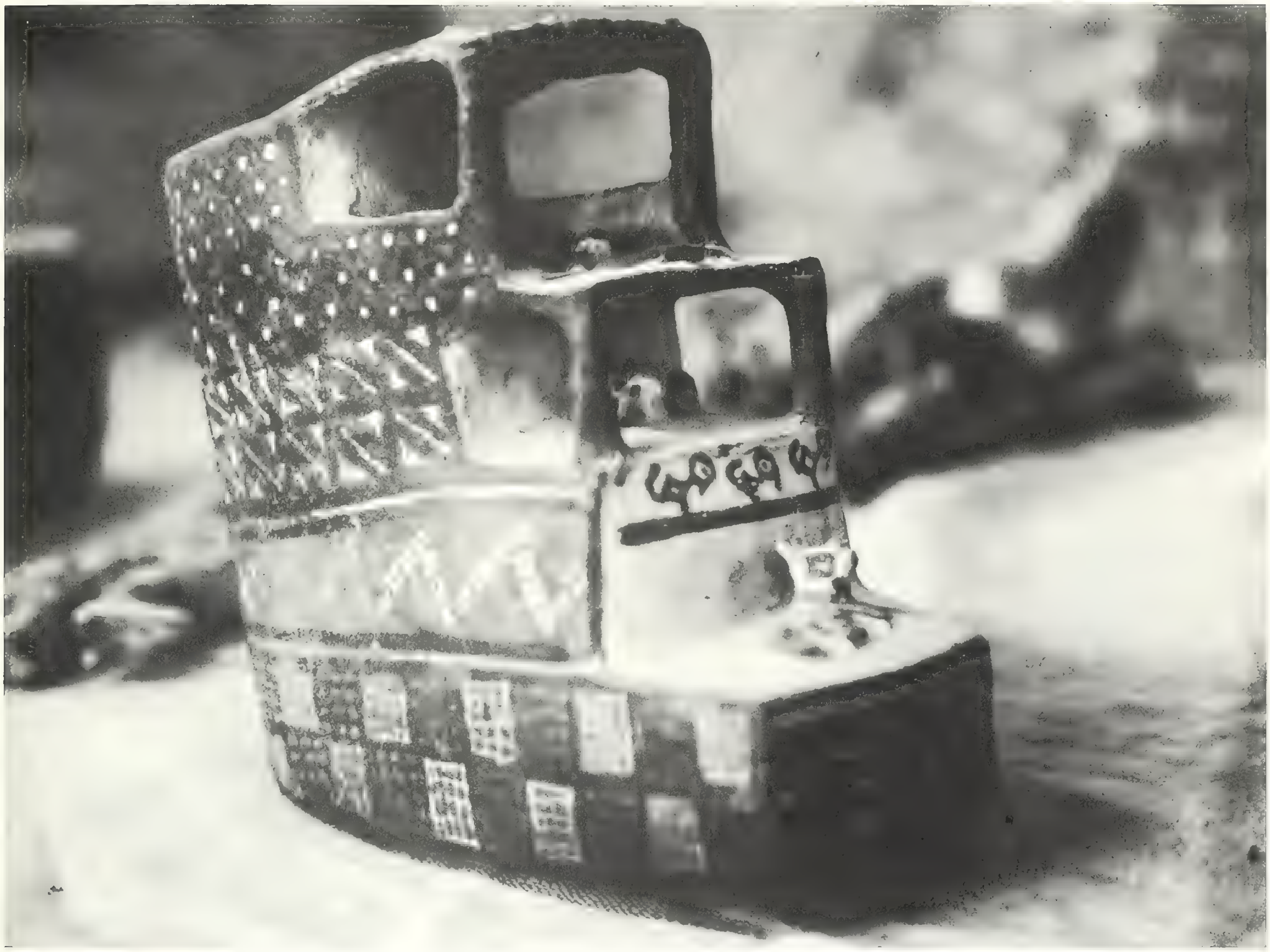

Fig. 18.—Ica 10 pot showing a structure similar to Building IV–1 and Room IV–1a at Lo Demás. This vessel is in the Museo Regional de Ica; photographed with permission of Sra. de Pezzia.

CHAPTER 7

CERAMIC VESSELS

This chapter discusses the late pre-Hispanic ceramic vessels from Lo Demás. Other categories of ceramic artifacts (figurines, spindle whorls, and "half-bobbin" objects) are considered in Chapter 8. Though small,[49] the pottery sample is still informative.

Compared with most ceramic-age sites which I have seen in Peru, Lo Demás seems to have a particularly low density of pottery, an observation supported by quantitative comparison of pottery density between the fishing site and a contemporary (late pre-Hispanic) farming site in the Chincha valley (Sandweiss, 1988:106; Table 4).

The sample of pottery from the excavations in primary deposits totals 3,552 sherds (Table 4), with 2,944 from Sector I (Subunits A1–3, B3, C3, 1A–D, 2A–D, 3A–D, 4A–D, 10B, and 10D) and 608 from Sector IV (Subunit 26D). The pottery from Room IV–1a is not included, because it is from a secondary context (fill). A sample of 1,690 sherds excavated by Patrick Carmichael of the Chincha–Pisco Archaeological–Historical Project in 1984 at the late pre-Hispanic farming site of Huacarones (PV 57–91) provides comparative data (Table 4). Huacarones is located in the Chincha valley some 10 km inland from Lo Demás (*see* Fig. 1).

Menzel's (1966) analysis of the late pre-Hispanic pottery excavated in Chincha by Max Uhle (1924;

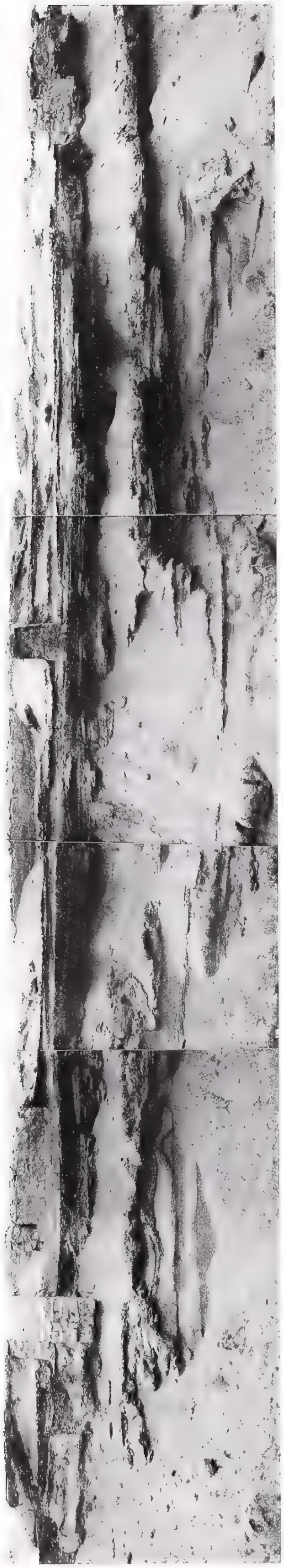

Fig. 19.—Composite photograph of the quebrada-cut east profile of Building IV–2, Sector IV, Lo Demás. The massive adobe walls cut perpendicularly to the quebrada at the left (south) and right center of the photograph are the south and north walls, respectively, of Building IV–2 (*see* Figs. 4 and 6). View is east to west.

Table 4.—*Sherds by fragment types, Lo Demás and Huacarones. Fragment types: 1, rim; 2, neck without rim; 3, body; 4, handle; 6, base; 7, support; 8, disk. Fragment type 5 was conflated with fragment type 4. Sherds which were too small to be analyzed (under 1 cm²) are not reported here.*

Complex	Fragment Type 1	2	3	4	6	7	8	Total
a) Lo Demás Sector I, all excavations.								
A	3	1	16	—	—	—	—	20
B	65	3	69	2	2	—	1	764
C	92	10	984	—	6	2	1	1,095
D	56	4	992	5	1	3	4	1,065
Total	216	18	2,683	7	9	5	6	2,944
b) Lo Demás, Sector IV, Subunit 26D.								
Total	63	3	535	2	1	—	4	608
c) Lo Demás, Sectors I and IV combined total.								
Total	279	21	3,218	9	10	5	10	3,552
d) Huacarones, Unit C total.								
Total	159	18	1,473	9	16	—	15	1,690

Kroeber and Strong, 1924) is particularly useful for two reasons. First, the Uhle sample consists mostly of whole vessels; I found no whole vessels in either Sector I or Sector IV of Lo Demás. Second, Menzel was able to construct a preliminary typology and sequence of late pre-Hispanic (Late Intermediate Period 8 and Late Horizon) vessels from Chincha; the Lo Demás sample is too small, and vessel form too poorly indicated by the available diagnostic sherds, to allow a reliable typology.

However, Menzel's typology provides only limited help with the Lo Demás pottery because 1) the Uhle sample came exclusively from tombs and does not include many vessels considered by Menzel as "utilitarian,"[50] whereas the entire Lo Demás sample discussed here came from midden context and consists mostly of vessels whose utilitarian or domestic nature is indicated by a high frequency of sooting; 2) Menzel concentrates on vessel form and discusses decoration only briefly and without illustration; and 3) the associations of diagnostic pottery from primary contexts at Lo Demás call into question some aspects of Menzel's division of late pre-Hispanic Chincha ceramics into two chronological groups, the "Chincha style" and the "post-Chincha assemblage" (Menzel, 1966:79 ff.).

METHODOLOGY

Variables on Lo Demás potsherds were recorded by Justo Cáceres M. and Elba Manrique M. (Cáceres M., 1984). Analysis of these data involved tabulating and comparing key variables by stratigraphic complex (in Sector I), by sector (I and IV), and by site (Lo Demás and Huacarones). Diagnostic features of the Lo Demás potsherds were also compared with the late Chincha vessels discussed by Menzel (1966) and with other late pre-Hispanic pottery, especially ceramics from nearby Ica (Menzel, 1976) and Inka wares from Cuzco (Rowe, 1944). Results are presented in two sections, on vessel use and on chronology and cultural affiliations. Data on use come principally from descriptive aspects of the sherd assemblages (including all morphologic categories) and from the reconstruction of vessel form using rim sherds. Data on chronology and cultural affinities are derived from the analysis of decoration, and to a lesser degree, vessel form.

VESSEL USE

The majority of sherds from both sectors (I and IV) come from cooking vessels; pottery apparently was also used for serving/eating, as liquid containers, for dry storage, and possibly for nondomestic purposes. In comparison, far fewer of the sherds from Huacarones come from cooking vessels; other uses of pottery at the farming site seem to have covered the same range as at Lo Demás, but with different emphases. Evidence for liquid containment at Huacarones is much less, whereas dry storage seems to have been more important.

Sooting

Exterior soot on potsherds from Lo Demás is the clearest indication that the primary use of pottery at the site was cooking. In most cases, the sherds are so heavily sooted or charred that they must certainly have been exposed to fire.[51] The frequency of exterior-sooted sherds for Sectors I and IV is almost identical (Table 5). Within Sector I, the frequency of exterior-sooted sherds from Stratigraphic Complexes A, B, C, and D differs by 12.5% at most, and the frequencies do not show a trend through time (Table 5).

Table 5.—*Count and percent of exterior sooting, all sherds, Lo Demás and Huacarones. The counts in this table include all sherds which were sooted on the exterior alone or on exterior and interior.*

	Count	Percent sooted
Sector I—Lo Demás		
Complex A	13/20	65.0
Complex B	445/764	58.2
Complex C	575/1,095	52.5
Complex D	654/1,065	61.4
I total	1,687/2,944	57.3
Sector IV—Lo Demás		
26D total	339/608	55.8
Huacarones		
Total	398/1,690	23.6

The frequency of exterior-sooted sherds from Huacarones is less than one half that in the Lo Demás sample (Table 5), suggesting that ceramic activities other than cooking (i.e., not involving fire-processing) were far more important in Huacarones than in Lo Demás. One possibility is that the inhabitants of Huacarones made greater use of pottery vessels for storage of agricultural products (Sandweiss, 1988), a hypothesis bolstered by data on sherd thickness and vessel form (*see below*). First, a caveat is in order: the Huacarones pottery sample came from a single excavation area on a large, artificial mound, while the Lo Demás sample came from a limited area in nonmonumental structures in Sector I and from the small test pit (Subunit 26D) adjacent to a large rectangular compound in the monumental part of the site (Sector IV) (*see* Chapter 5). Given the different contexts, these samples may not be directly comparable. However, the Lo Demás Sector IV sample has virtually the same percentage of sooted sherds as the Sector I sample (Table 5), yet comes from a context quite similar to the Huacarones excavation area. The uniform proportion of sooted sherds in all excavated areas of Lo Demás supports the interpretation that the differences in ceramics between Lo Demás and Huacarones reflect functional differences.

Sherd Thickness

Sherd thickness is difficult to measure and offers limited information. For the Lo Demás and Huacarones samples, each sherd was measured only once (in tenths of millimeters), on a representative edge, and all figures were rounded to the nearest millimeter. Even so, only the grossest of trends are likely to be meaningful, and the data need to be lumped into larger increment categories.

Preliminary inspection of the data suggests thicker sherds occur more frequently at Huacarones than at Lo Demás. Because storage vessels tend to be fairly large relative to cooking vessels, this observation is consistent with the hypothesis generated by the sooting data (*see above*) that more ceramics were de-

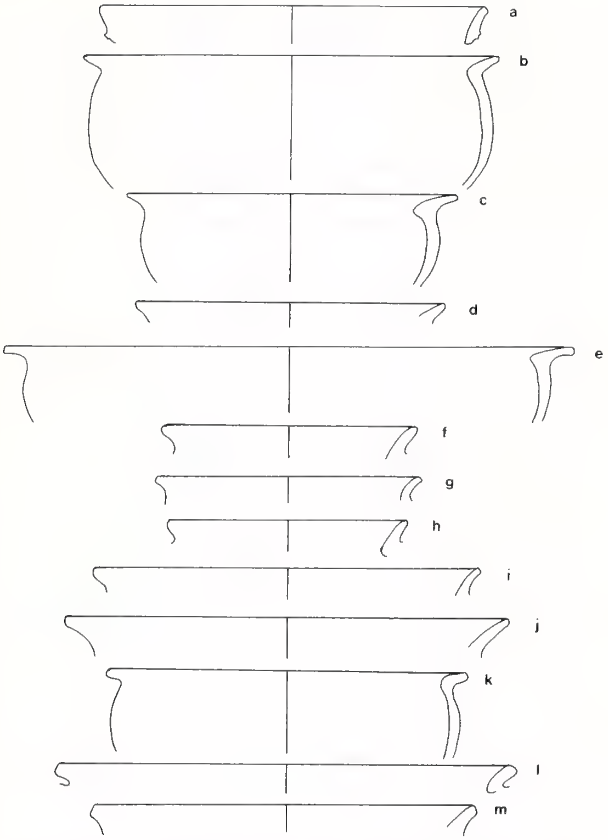

Fig. 20.—Angular rim bowl sherds from Lo Demás. Sector I: a–b (Stratigraphic Complex D), c–f (Complex C), g–j (Complex B); Sector IV: k–m. See text and Table 6 for further information.

voted to storage at Huacarones than at Lo Demás. Within the fishing site, results for Sector IV seem to be intermediate between Sector I and Huacarones, which makes sense given that Sector IV probably housed one of the local fishing lords: storage should concentrate around the lords, one of whose functions was the redistribution of goods to their subjects (*see* Chapter 2). According to the documents, specialists paid tribute in the goods "of their office." Under this system, lords of specialized groups would accumulate mainly the products of their group's specialty, both as the tribute the lords received for themselves and as the tribute which they paid to the Chincha and Inka lords on behalf of their group. Unlike agricultural produce, fish are not usually stored in pots (cf. Netherly, 1977:63), so fishing lords would have had less need for storage pottery than would farming lords.

Vessel Form

Whole vessels were not recovered from Sectors I and IV of Lo Demás, so almost all information on vessel form must come from the analysis of rim sherds (the ceramic collection includes very few other sherds which are diagnostic of form). Only 83 rim sherds are sufficiently preserved to allow measurement of the rim angle and diameter. Of these, not all preserve enough of the body to allow assignment to a shape category.[52] Nevertheless, seven basic shapes can be identified in the ceramic inventory from Lo Demás. The Huacarones sherd collection has 108 rim sherds sufficiently preserved to allow measurement of rim angle and diameter; the shape inventory is similar to that from Lo Demás.

Angular rim bowls.—This vessel shape is one of the most common in both the Lo Demás (Fig. 20, Table 6) and Huacarones collections (Sandweiss, 1989:191, Fig. 29, 186–188, Table 10); it is also the shape which can be reconstructed and assigned a use with the greatest confidence. Angular rim bowls have a wide orifice with a slight restriction or throat below a short, sharply everted rim or collar. Sherds assigned to this category have enough of the shoulder inflection to show the rim's shortness (relative to rim thickness and diameter) and sharp angle (from the vertical).

From the few examples for which total dimensions can be approximated, the rim diameter of Chincha angular rim bowls is somewhat more than twice the height; the maximum diameter of the vessel body is about the same as the rim diameter. Temper tends to be medium to medium fine. The collared jar specimens were all fired in an oxidizing environment;[53] paste color ranges from beige through red-orange to orange. Many of the specimens have an interior red slip (Table 6).

Three angular rim bowl rims were found in Subunit 26D in Sector IV and 10 in Sector I of Lo Demás (Fig. 20, Table 6); they were also present in many levels of the test unit at Huacarones.

All but one of the Lo Demás rim sherds that clearly fit the angular rim bowl category have exterior soot, indicating that this form was used as a cooking vessel. The shape fits the general criteria for a cooking pot rather well; such vessels tend to be short, squat, and not too large, with a wide base, a wide orifice, and a flaring or incurving lip (Costin, 1986: 205–207; *see also* Rice, 1987:236–241; Henrickson and McDonald, 1983:631). Rounded contours (Rice, 1987:237) and a slight constriction and/or low neck (Rice, 1987:239–240) are also desirable features for cooking vessels.

The form of the Lo Demás angular rim bowls is similar to that of the collared jars found in the Uhle collection (Menzel, 1966:85–86 and Plate X–14).

Although not illustrated, the one sooted utility vessel from the Chincha style burials seems to be an angular rim bowl identical to those from Lo Demás (*see* Sandweiss, 1989:190, footnote 125). In describing this vessel, Menzel succinctly describes the differences between the collared jars and angular rim bowls: "The collar [of the bowl] is much shorter and more everted and may be described more aptly as an everted rim" (Menzel, 1966:95). This vessel has a "heavily sooted bottom" (Menzel, 1966:95), indicating correspondence in use as well as form with the Lo Demás specimens. Menzel notes that the Cemetery B vessel came from a burial which also contained a "bottle/jar which probably predates the [LIP] Epoch 8 pottery" found in the other burials (Menzel, 1966:95). If this chronological attribution is correct, it would indicate that use of angular rim bowls for cooking is an old Chincha tradition clearly pre-dating the Inka conquest of the valley.[54]

Angular rim bowls are also a common feature of the Huacarones collection, which contains both sooted (9) and unsooted (13) specimens (Sandweiss, 1989:Fig. 29, Table 10). The fact that many Huacarones examples are unsooted suggests that angular rim bowls there had some use (perhaps serving) in addition to cooking. An alternative explanation is that some pots were broken before being put into use, but the fact that over half of the collared bowls from Huacarones are unsooted argues against this interpretation. The Huacarones angular rim bowl sherds have the same range of temper size, but the paste tends to be darker (mostly red-brown and grey-orange) than the Lo Demás examples. Some of the sooted specimens from Huacarones have an interior red slip, as at Lo Demás; many of the unsooted examples exhibit this feature on both interior and exterior surfaces.

The Huacarones angular rim bowl sherds include two examples which resemble an Ica 9 form (Menzel, 1966:Plate XII–35) found in a burial with Chincha style pottery (Sandweiss, 1989:Fig. 29a, b). This form, which Menzel (1976:36–37) calls the "Angular-Rim Dish," is diagnostic of the Late Horizon in Ica, as is the angular rim bowl form; as the names imply, the two vessel types are quite similar. One of the Lo Demás angular rim bowls also resembles slightly the angular rim dish form (Fig. 20h).

The Huacarones sherd sample includes several other angular rim bowl variants not seen in the Lo Demás assemblage (Sandweiss, 1989:195 and Figs. 29q–t, 30a, b).

Constricted bowls.—Constricted bowls are relatively common in the Lo Demás and Huacarones collections, though only one was found in Sector IV of Lo Demás (Fig. 21, Table 6) (Sandweiss, 1989: Fig. 32, Table 10). This vessel category is characterized by a constricted, neckless orifice, with the rim diameter notably less than the maximum diameter. On the few fairly complete profiles, vessel height and rim diameter seem about equal. Maximum width appears to be about 1.25 to 1.50 times vessel height and rim diameter; however, some rim sherds appear to come from taller vessels (narrower relative to height).

Of the 15 rim sherds from Lo Demás which can be assigned to the constricted bowl category, seven are sooted and eight are not (Fig. 21; Table 6). The sooted specimens range in rim diameter from 10 to 22 cm, while the unsooted fragments tend to have smaller diameters, measuring between 6 and 19 cm. Both sooted and unsooted sherds were fired in an oxidizing atmosphere. Paste on the sooted specimens tends to be orange, with one specimen each of red-brown and red-orange. Surface color ranges from orange to red-brown; one specimen has a red slip on the interior. Unsooted specimens have a greater variety of paste colors, including grey-red, brown-red, orange-red, orange, and tan. Surface colors include orange, brown-red, grey, and red; the red and grey are applied as interior and/or exterior slips.

All but one of the constricted bowls came from Sector I; the one example from Subunit 26D of Sector IV is unsooted. One heavily sooted specimen from Stratigraphic Complex B, Sector I, has a vertically-oriented, tubular handle with the upper end attached just below the lip (Fig. 21n). Menzel (1966: 88 and Plate XII–32) mentions only one vessel which could fall into the constricted bowl category; this pot came from Uhle's (1924) Cemetery B, directly east of Lo Demás Sector I. Menzel (1966:88) describes the vessel as a "*thinned rim bowl* with vertical convex sides" and places it in her LIP 8/early LH Chincha style.

Constricted bowls apparently had multiple uses at Lo Demás. The sooted vessels were employed in cooking. Lacking everted rims or lips, they were probably not used for cooking substances which could be poured. To use such vessels in cooking, direct access to the contents is necessary for stirring, etc. The sooted examples from Lo Demás range in orifice diameter from 10 to 22 cm, wide enough to allow direct access. The use of the unsooted examples is less obvious. All of the examples with smaller orifices (under ten cm diameter), which

Table 6.—*Rim sherds from Lo Demás illustrated in Figs. 20–23 and 25–27. Abbreviations: Fig., figure reference for this study; Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex in Sector I; Su, subunit; L/F, level or feature within excavation unit. Under Form: AR, angular rim bowl; CB, constricted bowl; WJ, wide-mouthed jar; RJ, restricted jar; Bt, bottle; OB, open bowl; PD, plate/dish. Under Paste and Surface: b, beige; br, brown; cr, cream; g, grey; o, orange; r, red; s, slip; ext, exterior; int, interior (if neither int or ext is specified, both surfaces are slipped). Under Temper: 1, coarse; 2, medium; 3, medium–fine; 4, fine. Under Soot: 0, no soot; 1, exterior soot; 2, interior soot; 3, soot on both sides. Diameter is in cm.*

Fig.	Cat.	SC	Su	L/F	Form	Paste	Surface	Temper	Soot	Diameter
					Sector I					
20a	6	D	A1	2a	AR	o	r-br	2	1	26
20b	788	D	4D	434b	AR	r-o	br	3	1	28
20c	1055	C	3D	7	AR	r-o	int r s	2	1	22
20d	1747	C	4D	494	AR	b	int r s	2	2	21
20e	1105	C	3D	7b	AR	o	g-o	2	1	38
20f	1755	C	4B	495	AR	r-o	int r s	2	1	17
20g	1350	B	10B	21	AR	g-o	r-o	2	3	18
20h	1242	B	3B	333	AR	r-o	int r s	2	1	16
20i	1077	B	10D	19	AR	b	g	2	3	26
20j	1469	B	3A	9b	AR	r-o	int r s	2	1	30
21a	16	D	A1	2ciii	CB	o	r-br	2	3	22
21b	6	D	A1	2a	CB	o	r-br	2	1	10
21c	17	D	A1	2ciii/d	CB	o	r-br	2	3	15
21d	633	D	2C	238	CB	r-o	ext r s	2	0	15
21e	580	D	2A	2cW	CB	b	int r s	2	0	14
21f	584	D	4D	4ic	CB	r-o	r s	2	0	12
21g	830	C	10D	14	CB	r-o	r-o	2	1	16
21h	888	C	3B	6	CB	g core	g-o	2	1	19
21i	57	C	A3	3bii	CB	g-o	g	2	0	7
21j	1631	C	4D	14i	CB	b	g	3	0	6
21k	1418	B	10D	1040	CB	r-br	int r s	2	1	15
21l	1418	B	10D	1040	CB	o	o	2	1	15
21m	1621	B	2B	13ib-id	CB	g-o	ext g s	2	0	7
21n	1844	B	4B	II409	CB	r-o	r-o	2	1	14
22a	42	D	B3	2b	WJ	o	o	2	0	48
22b	536	D	10D	2	WJ	r-br	int r s	2	1	26
22c	888	C	3B	6	WJ	r-br	r-br	2	1	38
22d	1500	C	2C	10i	WJ	r-br	r-br	1	0	37
22e	1075	C	3B	330b	WJ	g core	r-br	2	0	36
22f	731	C	1A	10W	WJ	r-o	rp s	2	0	28
22g	1690	C	4B	485	WJ	r-o	int r s	2	1	27
22h	1731	B	2C	15	WJ	r-o	int r s	2	0	30
23a	931	D	4C	5b	RJ	r-o	ext g s	2	0	20
23b	17	D	A1	2d	RJ	r-br	r-br	2	1	22
23c	533	D	4C	4	RJ	r-br	r-br	2	1	14
23d	690	C	10B	7	RJ	b	b	2	0	14
23e	817	C	1C	117	RJ	r-br	r-br	2	1	18
23f	1621	B	2B	13ib-id	RJ	r-o	ext r s	2	0	22
23g	1731	B	2C	15	RJ	r-o	int r s	3	1	19
23h	1621	B	2B	13ib-id	RJ	o	r s	2	2	19
23i	1847	B	4B	24i	RJ	o	r s	2	0	10
23j	1535	B	3B	12	RJ	b	b	3	0	13
23k	1563	B	3D	9b	RJ	r-o	r-o	2	0	20
23l	1201	B	1C	25W	RJ	r-o	r-o	3	0	9
23m	1621	B	2B	13ib-id	RJ	r-o	ext r s	1	0	16
23n	1086	B	10B	19	RJ	r-o	r-o	2	0	12
23o	1850	B	4D	25	RJ	o	o	3	0	19
23r	1201	B	1C	25W	RJ	r-o	r-o	3	0	9
23t	1641	C	4B	14	RJ	g core	o	3	0	9
25a	1184	D	4B	440	Bt	r-o	r-o	3	0	6
25b	1706	C	4D	17i	Bt	o	o	3	0	8
25c	818	C	2B	7b	Bt	o	int r s	3	0	5

Table 6.—*Continued.*

Fig.	Cat.	SC	Su	L/F	Form	Paste	Surface	Temper	Soot	Diameter
25d	1426	C	2C	8b	Bt	o	ext r s	4	0	7
25e	834	C	2B	8b	Bt	r-o	r-o	3	0	6
25f	1477	C	4D	9	Bt	g	g	3	0	8
25g	810	C	3B	5c	Bt	b	b	3	0	2
25h	1847	B	4B	24i	Bt	o	r s	2	0	6
25i	1742	B	2C	292	Bt	b	r s	3	0	7
25k	1253	C	2A	262b	Bt	r-o	r-o	2	1	8
26a	10	D	A2	2b	OB	g-o	g-o	2	0	24
26b	19	D	A2	2d	OB	r-br	ext r s	2	0	18
26c	18	D	A2	2d	OB	r-br	ext r s	2	1	18
26d	767	D	4B	5	OB	o	r s	2	1	21
26e	82	D	A2	f17	OB	o	r-br	2	1	26
26f	17	D	A1	2b–d	OB	r-br	ext r s	2	0	18
26g	428	D	3A	3	OB	r-o	r-o	3	1	14
26h	1535	B	3B	12	OB	b	b	2	0	18
26i	1850	B	4D	25	OB	o	r-o	2	0	20
26l	1647	C	4B	479	OB	g-o	ext cr s	3	0	13
27a	1193	B	1C	26W	PD	r-o	r-o	3	0	17
27b	1827	B	4D	23i	PD	r-o	int r s	3	0	24
					Sector IV					
20k	1831		26D	12b	AR	b	int r s	2	1	24
20l	1858		26D	16	AR	r-br	r-br	2	1	30
20m	1858		26D	16	AR	o	int r s	2	1	26
21o	1841		26D	13	CB	o	o	3	0	8
22i	1717		26D	3	WJ	r-o	int r s	2	0	29
23p	1852		26D	13bi	RJ	r-o	r-o	3	0	20
23q	1851		26D	13b	RJ	o	o	3	0	20
23s	1743		26D	5c	RJ	g-o	int r s	2	1	15
25j	1800		26D	10	Bt	r-o	r-o	2	0	7
26j	1717		26D	3	OB	r-o	int r s	2	1	14
26k	1853		26D	14b	OB	g	g	3	0	10
27c	1726		26D	5	PD	r-o	o	3	0	23

would be inconvenient for stirring or other manipulation during cooking, are unsooted.

The constricted bowl form is appropriate for cooking and for serving and eating: vessels in both functional categories tend to be short and squat for stability, to have a relatively wide orifice for ease of access, and to have a slight restriction at the orifice to avoid spills (Costin, 1986:205–207; Henrickson and McDonald, 1983:631–632).[55] In contrast, the constricted bowls do not fit the criteria for storage vessels very well. Long-term dry storage containers tend to be tall and thin, with more restricted orifices than the constricted bowls and with an everted or rolled rim (Henrickson and McDonald, 1983:632–633; Costin, 1986:207–208). Short-term dry storage vessels tend to be wider (Henrickson and McDonald, 1983:362–363). Wet storage vessels intended for both long- and short-term storage tend to be tall and thin, with rolled or everted rims; highly constricted openings are not particularly common (Henrickson and McDonald, 1983:363; Costin, 1986:207–209). In light of these ethnographic data, it is possible that in addition to cooking, the constricted bowls at Lo Demás were used for consumption (serving and/or eating) and perhaps for short-term storage of dry goods. Some of the vessels could have been used in sequence for cooking, serving, eating, and storing the same contents, while others served only some of these uses; as Rice (1987: 232–233) points out, "vessels typically have multiple uses during their life spans."

At Huacarones, 14 examples of constricted bowls were recovered (Sandweiss, 1989:Fig. 32, Table 10); one is exterior-sooted and the rest are unsooted. The unsooted specimens have rim diameters ranging from 7 to 23 cm, similar to the overall range of the Lo Demás constricted bowls. The exterior-sooted specimen has a rim diameter of 18 cm. The recon-

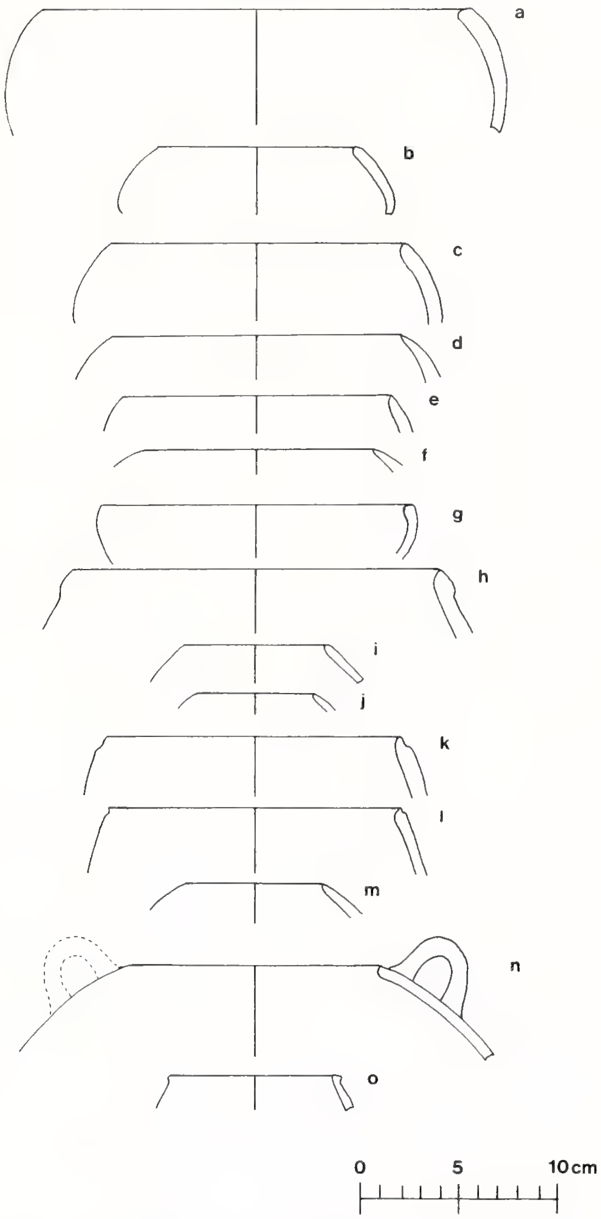

Fig. 21.—Constricted bowl sherds from Lo Demás. Sector I: a–f (Stratigraphic Complex D), g–j (Complex C), k–n (Complex B); Sector IV: o. See text and Table 6 for further information.

structed dimensions of the Huacarones constricted bowls seem to be about the same as those from Lo Demás; as at the fishing site, a few examples from Huacarones appear to come from straighter-sided, narrower vessels. The Huacarones constricted bowls do not shed any additional light on the use(s) of this vessel category in Chincha.

Jars.—Menzel (1966:81) writes that for her LIP 8/early LH Chincha style fancy ware, "by far the most common category . . . consists of jars with necks." Necked vessels also occur in Menzel's (1966) late LH post-Chincha Assemblage, though with less frequency and a greater variety of forms. Jars with necks are quite common in the Lo Demás pottery assemblage.[56] None of the jar neck sherds retain any significant portion of the body, so it is impossible to determine the shape(s) of the jars; variation in rim size and neck form allow some differentiation. I have tentatively classified necked vessels into three categories based on rim diameter: wide-mouthed jars (diameter $\geq$ 25 cm), restricted jars (diameter $<$ 25 cm and $>$ 8 cm), and bottles (diameter $\leq$ 8 cm).

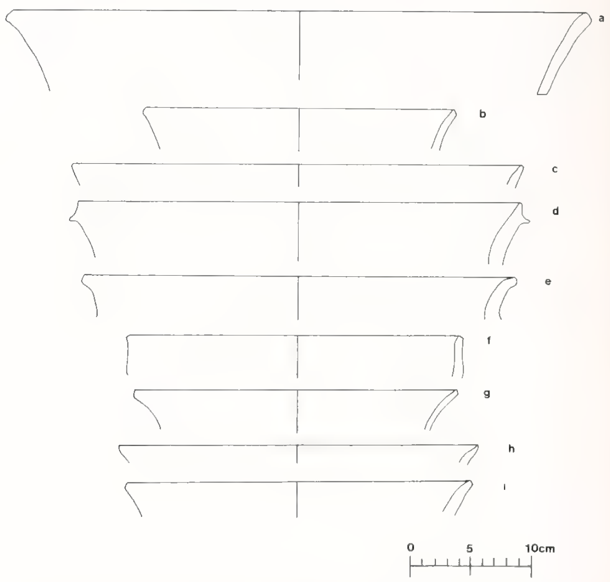

Fig. 22.—Wide-mouthed jar sherds from Lo Demás. Sector I: a, b (Stratigraphic Complex D), c–g (Complex C), h (Complex B); Sector IV: i. See text and Table 6 for further information.

Wide-mouthed jars.—Rim sherds assigned to this category have a diameter of 25 cm or more and are everted or flaring. The rim diameter on these vessels seems to be slightly greater than the throat diameter. Wide-mouthed jar sherds were distinguished from angular rim bowl sherds by a longer (relative to width and diameter) and more vertical (less sharply everted) rim. Nine sherds from Lo Demás are classified as wide-mouthed jars (Fig. 22; Table 6); six are unsooted and three are sooted. The unsooted rims tend to be thicker and to have a wider diameter than the sooted rims. Only one of the wide-mouthed jar neck sherds has the corner point where the neck joins the shoulder of the vessel (Fig. 22e), and it is possible that the other sherds actually came from large dishes or basins. Menzel (1966) does not illustrate any late pre-Hispanic Chincha vessels with a rim diameter of 25 cm or greater, so her work offers no guide to reconstructing this vessel category.

Both sooted and unsooted wide-mouthed jar sherds were fired in an oxidizing atmosphere. The sooted sherds have a red-brown or red-orange paste; two have an interior red slip. Rice (1987:241) notes that a "slip over the mouth and rim area makes cleaning easier," an important characteristic for cooking, eating, and serving vessels. The unsooted specimens include the same paste colors in addition to one orange paste sherd and one incompletely oxidized sherd with a grey core. Two of the unsooted sherds have an interior red slip, one has an exterior red slip, and one has a red-purple slip on both surfaces. Rim diameters for the sooted sherds are 26, 27, and 38 cm, while the unsooted rims range from 28 to 48 cm in diameter. All but one of the wide-mouthed jar sherds came from Sector I; the one exception, an unsooted specimen, came from Subunit 26D in Sector IV.

The sooted wide-mouthed jar sherds come from vessels presumably used for cooking. The shape of two of these sherds (Fig. 22a, b) resembles the collar on a Chincha style collared jar illustrated by Menzel (1966:Plate X–14).[57] This collared jar is related morphologically to the Lo Demás angular rim bowls described above, the only significant differences being the greater height of the jar's collar and the higher value of the height to width ratio for the jar. The angular rim bowls at Lo Demás were used for cooking (*see above*).

Because overall proportions of the Lo Demás wide-mouthed jars cannot be reconstructed, the use of the wide-mouthed vessels which produced the unsooted sherds is less clear than the case of the sooted sherds. Some probably were storage vessels; the wide mouths and throats of these vessels would facilitate access to the contents, an important characteristic for many dry goods which are not easily poured (Henrickson and McDonald, 1983:632; Costin, 1986:207–208; Rice, 1987:240–241).

One unsooted, wide-mouthed sherd from Sector I of Lo Demás has a labial flange (Fig. 22d) and another has a sharply everted rim (Fig. 22e), characteristics which are useful for tying covers over storage vessels (Henrickson and McDonald, 1983: 632; Costin, 1986:207–208; Rice, 1987:241). In their survey of the ethnographic literature, Henrickson and McDonald (1983:632) found that "almost all the long-term [dry storage] vessels have rolled-over or everted rims." Of the 22 wide-mouthed jar sherds from Huacarones (Sandweiss, 1989:Table 10), nine have a labial flange (Sandweiss, 1989:Fig. 34a–i) and four have a sharply everted lip (Sandweiss, 1989: Fig. 34j–m). Nineteen of the Huacarones sherds in this category are unsooted (including eight of the flanged sherds and three of those with sharply everted lips). Three are sooted, one (with labial flange) on the interior, one on the exterior, and one on both surfaces. The wide-mouthed jar sherds with labial flanges are the thickest rim sherds from either site.

Restricted jars.—This category includes all necked vessels with rim diameters between 25 and 8 cm (not inclusive). Inspection of the illustrations shows that this general classification subsumes a number of types, all of which have everted rims. Like the wide-mouthed jar sherds, the restricted jar sherds were distinguished from the angular rim bowl sherds by a longer (relative to width and diameter) and more vertical (less sharply everted) rim. The Lo Demás pottery assemblage includes 20 rim sherds in this category, 17 from Sector I and three from Sector IV (Fig. 23; Table 6). Six of the specimens are sooted and 14 are unsooted.

All of the sooted restricted jar sherds and most of the unsooted specimens were fired in an oxidizing atmosphere; paste color ranges from orange through red-orange to red-brown and tan. One unsooted example has a grey core, indicating incomplete oxidation, and another has grey paste, suggesting that it was fired in a reducing atmosphere. Three examples (two sooted, one unsooted) have an interior red slip, one (unsooted) has an exterior red slip, one (unsooted) has an exterior grey slip, and two (one sooted, one unsooted) have a red slip on both surfaces. Four sherds have a design in dark brown or black on the interior of the rim (Fig. 23f, p, r, s); Menzel (1976:117 ff; *see also* Menzel, 1966:92) refers to this design as the "Chincha Rim Scallop" (*see below,* sections on Bottles and Pottery Decoration). Temper in the restricted jars tends to be medium–coarse, although several examples have a medium–fine temper. The sherds decorated with the Chincha Rim Scallop comprise most of the medium–fine temper specimens.

Two of the sooted restricted jar sherds (Fig. 23h, i) and one of the unsooted sherds (Fig. 23j) have the corner point, and five others (two sooted, three unsooted) are broken close enough to the shoulder to confirm that they came from necked vessels with shoulders (i.e., jars) (Fig. 23a, c, e, k, q). Menzel (1966:92) found that in the Uhle Chincha collection, two vessel categories "invariably" had the Chincha Rim Scallop design: complex rim bowls (a highly distinct form not found in the Lo Demás collection) and jars. Several jar neck sherds and one bottle neck collected from the quebrada adjacent to Sector IV of Lo Demás also had the Chincha Rim Scallop (Fig. 24), so it is reasonable to assume that the rim sherds with this design in the Lo Demás excavation sample also came from jars or bottles, depending on rim diameter.

Six of the restricted jar rims (Fig. 23e, g–k) are quite similar to the rims on ovoid jars (both high and squat types) discussed and illustrated by Menzel (Menzel, 1966:81–84 and Plates IX–XI). Ovoid jars are typical of Menzel's LIP 8/early LH Chincha style. One of the unsooted Lo Demás ovoid jarlike sherds has a marked labial flange (Fig. 23k); one unsooted (Fig. 23l) and two sooted sherds have weakly defined flanges (Fig. 23e, i). The reduced-fired sherd is highly everted (Fig. 23q). One unusual rim (Fig. 23t) has an everted lip.

The sooted sherds most likely come from vessels used for cooking. Rice (1987:241) states that a "restricted orifice . . . retards evaporation of the contents during prolonged heating," which suggests that the restricted jars were used to cook foods intended to maintain more of their water content than the foods cooked in angular rim bowls and wide-mouthed jars. The food cooked in the constricted bowls might have fallen somewhere in between that of the other two categories in terms of desired moisture content. The unsooted vessels could have been used for storage and/or serving, especially of pourable contents such as liquids and small grains. The relatively restricted orifice of these vessels would make them inconvenient for the storage of materials which required frequent, direct access. However, a restricted orifice also makes the opening easier to cover. In cooking, this attribute would further retard evaporation; for storage, covering provides additional protection to the contents at the cost of less convenient access.

The clearly defined labial flange occurs on an unsooted rim (Fig. 23k); flanges and everted rims may have aided in attaching a pliable cover to the jar

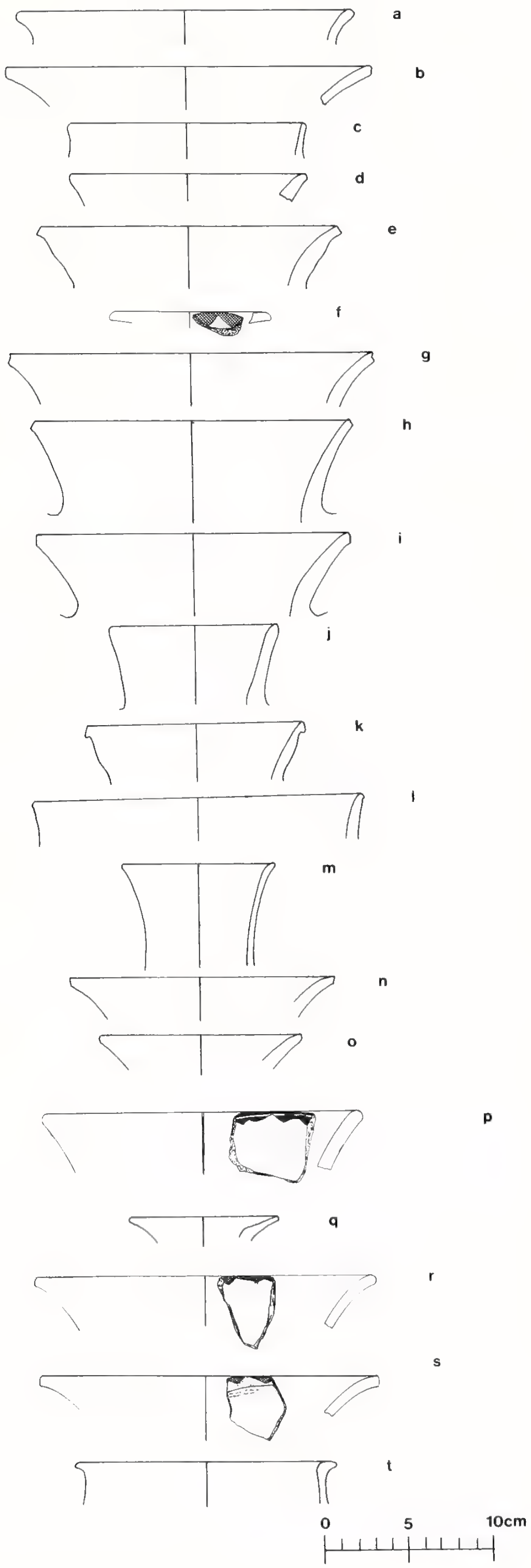

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Fig. 23.—Restricted jar sherds from Lo Demás. Sector I: a–c (Stratigraphic Complex D), d–f (Complex C), g–q (Complex B); Sector IV: r–t. See text and Table 6 for further information. See Fig. 28 for color key.

(Henrickson and McDonald, 1983:632; Rice, 1987: 241). The fact that five of the six sooted sherds (Fig. 23b, e, h, i, t) in the restricted jar category are sufficiently everted to attach a cover provides another indication that pottery vessels at Lo Demás probably had multiple uses during their lifespan.

The Huacarones collection includes 17 sherds which fall into the restricted jar category on the basis of rim diameter and form (Sandweiss, 1989:Fig. 37, Table 10). Four are sooted and 13 are unsooted. One of the unsooted sherds is very thick and has a labial flange very similar to those on the Huacarones wide-mouthed jars (Sandweiss, 1989:Fig. 37b). Two thinner, unsooted sherds also have labial flanges, though of rather different shapes (Sandweiss, 1989: Fig. 37n, o). One of the sooted sherds has a flange-like thickening of the exterior of the lip (Sandweiss, 1989:Fig. 37p). Four sooted and two unsooted specimens have sharply everted lips (Sandweiss, 1989: Fig. 37c–f, j, l). One unsooted rim sherd has a variant of the Chincha Rim Scallop design feature (Sandweiss, 1989:Fig. 37e). Like the Lo Demás collection, the Huacarones restricted jar sherds suggest multiple uses for this vessel category, including cooking and storage.

Bottles.—This category covers all of the restricted neck vessels with rim diameters of 8 cm or less. Eleven sherds from Lo Demás fit this category, one from Sector IV and ten from Sector I (Fig. 25; Table 6). Only one bottle rim sherd is sooted. All examples have mildly to sharply everted rims, so the minimum orifice diameter is always less than the rim diameter.

All but one of the bottle rim sherds were fired in an oxidizing atmosphere. The exception is a sharply everted, 8 cm diameter, reduced-fired rim with grey paste and surface (Fig. 25g). The oxidized sherds have orange, red-orange, or tan paste. Temper tends to be medium–fine, though a few examples have medium–coarse temper and one has fine temper. One rim has an exterior red slip and one has an interior red slip; two sherds have a red slip on both surfaces. Two rims have the Chincha Rim Scallop design in dark brown on the interior of the rim (Fig. 25a, j); one of these sherds has a red slip on both surfaces. A complete bottle rim and neck from the surface of the quebrada adjacent to Sector IV of Lo Demás has the Chincha Rim Scallop (Fig. 24d).

Five of the bottle rim sherds have at least indications of the corner point (Fig. 25b, d, f, h, i), although none include part of the body. These sherds all indicate a fairly short neck, similar in this respect to the Chincha vessels classified as flasks by Menzel (1966:Plate XI–17, 18).

In terms of use, the general lack of sooting and the very narrow orifice of the bottles indicates that they could only have been used to contain pourable contents, most probably liquid. Direct access to the

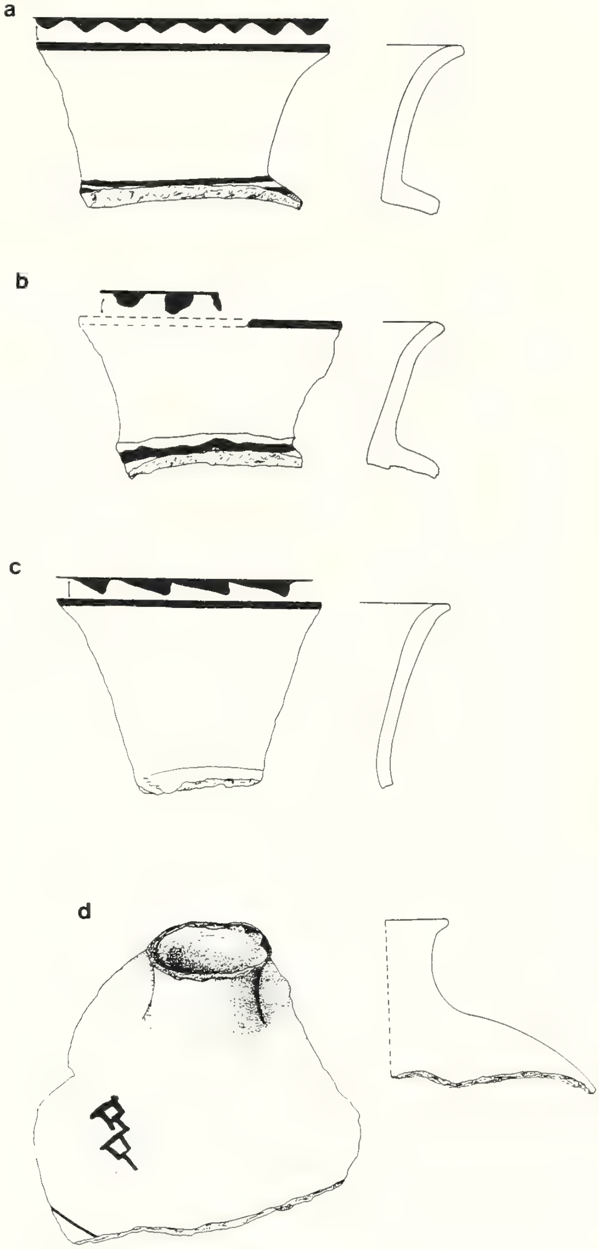

Fig. 24.—Sherds from the quebrada to east of Sector IV, Lo Demás. All are unsooted, are made of pure orange paste with medium–fine temper, and have an exterior red slip and black pendent triangles on the interior of the rim. Rim diameters are (from a to d): 13, 11, 14, and 5 cm.

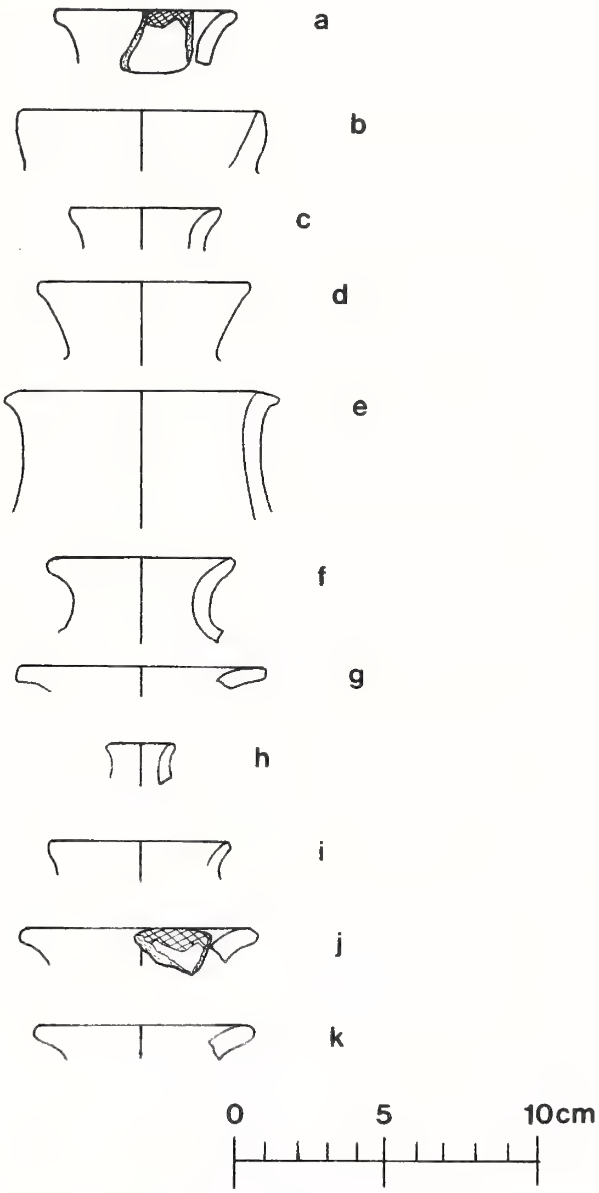

Fig. 25.—Bottle sherds from Lo Demás. Sector I: a (Stratigraphic Complex D), b–h (Complex C), i, j (Complex B); Sector IV: k. See text and Table 6 for further information. See Fig. 28 for color key.

contents was not possible. Whether they were used for long- or short-term storage (or both) is difficult to determine. Long-term liquid storage vessels tend to be larger than short-term ones (Henrickson and McDonald 1983:633). Although the overall dimensions and capacity of the Lo Demás bottles cannot be determined from the available sherds, the closest analogues in the Uhle collection (Menzel, 1966) are not very large,[58] and some of the Lo Demás bottle rim sherds are quite thin (4 to 8 mm). Both facts suggest that the Lo Demás bottles were small and therefore probably intended for short-term storage of liquids. The ease with which the small orifices of bottles can be stoppered, however, suggests that they *could* have been used to store liquids for a long time.

The Huacarones collection has only one sherd with the appropriate rim diameter to fit the bottle category (Sandweiss, 1989:Fig. 42a, Table 10). This sherd has a straight lip, a nubbin or lug about 1.5 cm below the lip, and a neck bulge beginning at the nubbin. This shape has no analogue in the Uhle Chincha or Ica collections (Kroeber and Strong, 1924; Menzel, 1966, 1976).

Open bowls.—This category is one of the most difficult to identify; most of the sherds assigned to it could be everted rims from necked or collared vessels. The identifying characteristics are a convex shape and no indication of a corner point; it is the latter characteristic which I used to distinguish open bowl sherds from angular rim bowl sherds. Rim diameter is necessarily the maximum diameter on such vessels. I have tentatively placed 12 sherds from Lo Demás in this category, ten from Sector I and two from Subunit 26D in Sector IV (Fig. 26; Table 6). Five sherds are sooted, including one from Sector IV.

Most sherds assigned to the open bowl category were fired in an oxidizing atmosphere, although one grey paste, unsooted specimen was fired in a reducing environment, and one grey-orange paste, unsooted sherd was incompletely oxidized. Paste color on the oxidized sherds is variable and includes orange, red-orange, red-brown, and tan. Three sherds have a red slip on the exterior, one on the interior, and one on both surfaces. One sherd has an exterior cream slip with a dark brown, painted, geometric design (Fig. 26h). Temper tends to be medium–coarse, with a few medium–fine temper examples.

Menzel illustrates only a few convex-sided bowls and dishes,[59] two from her LIP 8/early LH Chincha style (Menzel, 1966:Plate XII–33, 35) and two Inka/imitation Inka examples from her LH post-Chincha assemblage (Menzel, 1966:Plate XV–63; Plate XVI–79). The Lo Demás sherds do not resemble any of these examples, though the small size of the sherds limits comparison. Four of the Lo Demás specimens (Fig. 26a–c, k) exhibit some variation of a characteristic not seen on any of the Chincha pottery illustrated by Menzel (1966) or Kroeber and Strong (1924). Referred to by Cáceres M. (1984) as "borde semi-ampuloso," this feature consists of an undulating outer profile below the lip. The inner profile is rarely affected and usually shows a smooth, convex curve. Two other sherds (Fig. 26d, i) have related forms in which the inner profile is also undulating.

The sooting on five open bowl sherds suggests that the vessels they represent were used for cooking. The unsooted specimens probably functioned as serving and/or eating vessels. Henrickson and McDonald (1983:632) describe the typical serving/eating vessel as having "the maximum diameter . . . equivalent to the rim diameter, resulting in open, 'unrestricted' bowls." Furthermore, the wide orifice and probably small volume of the Lo Demás open bowls would not be well suited for storage. Average rim diameter of serving/eating vessels varies according to whether the vessel is intended for an individual or a family (Henrickson and McDonald, 1983). The average rim diameter of the Lo Demás sherds is about 18 cm, midway between Henrickson and McDonald's figures for family and individual vessels.

The Huacarones collection includes 28 sherds assigned to the open bowl category, of which three have exterior soot and 25 are unsooted (Sandweiss, 1989:Fig. 40, Table 10). At least four of the unsooted specimens are sufficiently preserved to make their assignment to the open bowl category fairly secure; three of these sherds (Sandweiss, 1989:Fig. 40a–c) are from vessels which appear to be cumbrous bowls (Menzel, 1976:45–47, 1966:Plates 13–45). Although this vessel form is common in the LIP/LH Ica pottery tradition, the Uhle Chincha collection did not contain any examples (Menzel, 1966:102). One of the Lo Demás open bowl sherds also resembles a cumbrous bowl (Fig. 26f).

Eight of the Huacarones open bowl sherds (all unsooted) exhibit variations of the "semi-ampuloso" or undulating profile (Sandweiss, 1989:Fig. 40d–g, i–l). These sherds are thick, like their Lo Demás counterparts; however, the exact forms of the profiles in the Huacarones sample are visibly different from the Lo Demás rims. A principal difference is that both the inner and the outer profiles of the Huacarones bowls are inflected, while most of the Lo Demás sherds show this feature only on the exterior profile.

The three exterior-sooted Huacarones open bowl rims (Sandweiss, 1989:Fig. 40l–n) are also thick (average = 8.7 mm), as are the cumbrous bowl rims (average = 6.0 mm), the "semi-ampuloso" rims (average = 8.8 mm), and four other unsooted open bowl rims (average = 6.0 mm) (Sandweiss, 1989:Fig. 40o–q, bb). However, 11 of the unsooted Huacarones open bowl rims (average = 4.5 mm) (Sandweiss, 1989:Fig. 40r–aa) are noticeably thinner than the Lo Demás sooted or unsooted specimens (average = 7.0 mm and 6.3 mm, respectively). The thin walls of these Huacarones bowls are consistent with use for serving/eating; storage vessels generally require fairly thick walls for strength and durability, while light weight would be an advantage for a serving or eating vessel.

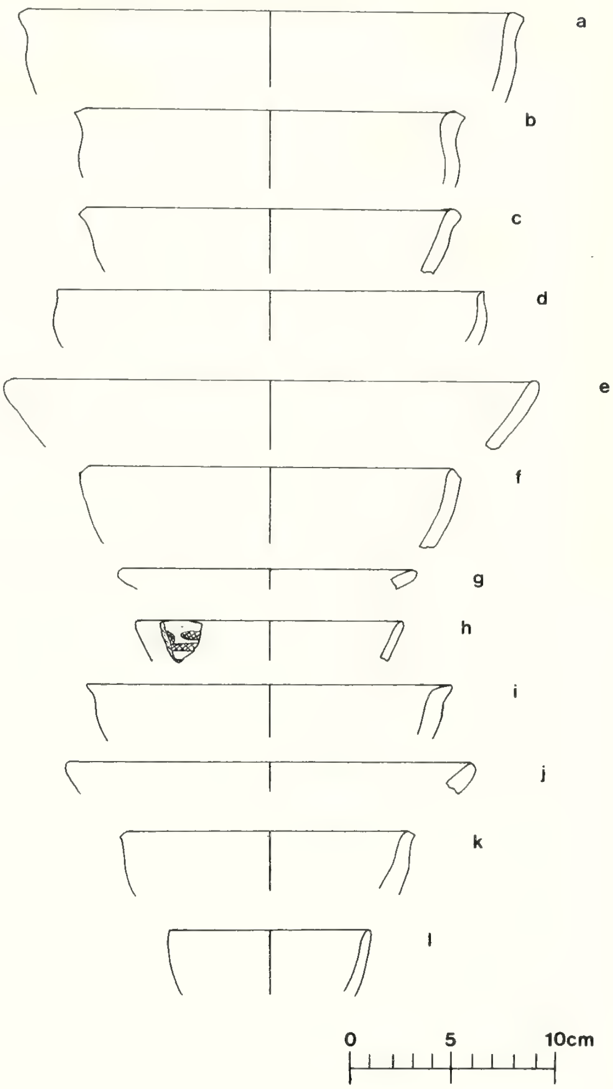

Fig. 26.—Open bowl sherds from Lo Demás. Sector I: a–g (Stratigraphic Complex D), h (Complex C), i, j (Complex B); Sector IV: k, l. See text and Table 6 for further information. See Fig. 28 for color key.

One of the thicker Huacarones open bowl rims

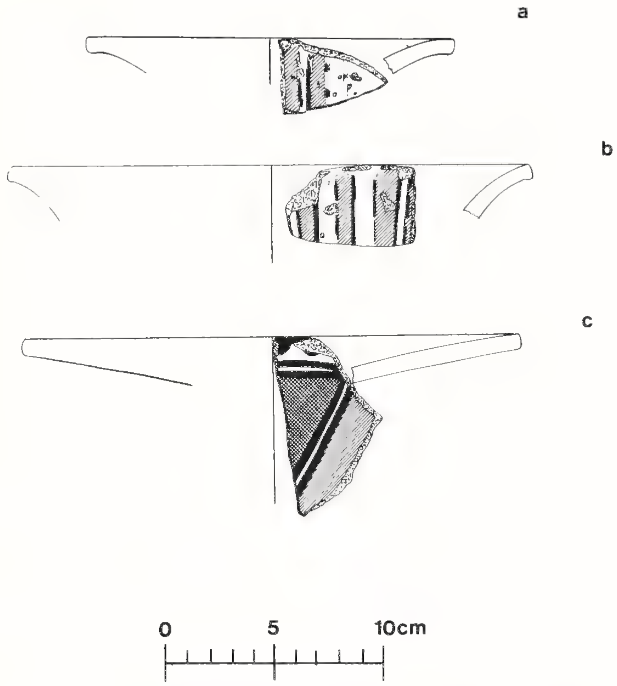

Fig. 27.—Plate/dish sherds from Lo Demás. Sector I: a, b (Stratigraphic Complex B), Sector IV: c. See text and Table 6 for further information. See Fig. 28 for color key.

(Sandweiss, 1989:Fig. 40bb) has a variant of the Chincha Rim Scallop design feature on the interior of the rim (Menzel, 1976:117 ff.) (*see* sections on Restricted Jars, Bottles, and Painted Decoration).

Plates/dishes.—Plates and dishes are open, shallow vessels with open (everted) sides (dishes are somewhat deeper than plates). The three fragments from Lo Demás assigned to this category (Fig. 27a–c; Table 6) are the only decorated rim sherds other than the six restricted jar and bottle specimens with the Chincha Rim Scallop and one open bowl fragment with a geometric design. None of the plate fragments is sooted.

Two plate sherds from Stratigraphic Complex B in Sector I are decorated on the interior with polychrome lines running perpendicular to the rim (Fig. 27a, b). One of these sherds appears to come from a very shallow vessel, while the other is deeper. The closest published analogue for this decoration is to LH Ica 9 pottery (*see below,* section on painted decoration).

The third plate sherd from Lo Demás was found in Subunit 26D in Sector IV (Fig. 27c); this rim comes from a shallow Inka (or imitation Inka) plate (B. Bauer, personal communication, 1988). Decoration is in white, black, light brown, and weak red (*see below,* section on painted pottery decoration). Temper is medium–fine, paste is red-orange, and the unpainted surface is orange.

Plates and dishes are most often used for serving and eating; their shape fits the criteria for this function outlined by Henrickson and McDonald (1983: 632) while offering little utility for storage. The presence of interior decoration on the Lo Demás sherds is a further indication that the vessels they represent were used for serving; as Rice (1987:240) explains, "because vessels for serving and eating are usually used in company, they may display fine surface finishing and elaborate decoration."

The Huacarones sample has two sherds which can be classified as plates or dishes (Sandweiss, 1989: Fig. 41d, e, Table 10). Both are unsooted, neither is decorated. One rim has a fairly smooth profile, while the other exhibits the "semi-ampuloso" or undulating profile seen on some of the Huacarones open bowls.

Summary of Vessel Forms by Stratigraphic Complex, Sector, and Site

Table 7 shows the distribution of vessel shape categories by stratigraphic complex in Sector I of Lo Demás, by sector (I vs. IV) at Lo Demás, and by site (Lo Demás versus Huacarones). In Sector I of Lo Demás, the majority of open bowls occurred in Complex D, while most of the wide-mouthed jars and most of the bottles were found in Complex C. Complex B contained the majority of the restricted jars. In each of these cases, the indicated shape category(ies) is/are the predominant vessel form within the complex. The other categories are fairly evenly distributed in the different complexes. In Subunit 26D in Sector IV, each shape category is represented by one to three examples. This sector and Sector I (taken as a total) have a similar distribution of shapes. Despite these apparent patterns, however, the small size of the sample for each complex and for Subunit 26D, in addition to the tentative nature of many sherd assignments, requires caution in using these results. Furthermore, the probable multiple uses of most shape categories suggest that the variations in proportion of categories may have little to do with the ways in which pottery was employed at Lo Demás. Each major stratigraphic complex (B to D) in Sector I, as well as Subunit 26D in Sector IV, has vessels which were or could have been used for storing, cooking, and serving/eating. These functional categories correspond to the three broader "realms" of domestic ceramic container use defined by Rice

Table 7.—*Distribution (counts/percents) of rim sherds by vessel shape category, Lo Demás and Huacarones. Shape categories: AR, angular rim bowls; CB, constricted bowls; WJ, wide-mouthed jars; RJ, restricted jars; Bt, bottles; OB, open bowls; PD, plates/dishes; U, unique shapes.*

	AR	CB	WJ	RJ	Bt	OB	PD	U	Total
				Lo Demás—Sector I					
Complex B	4/15.4	4/15.4	1/3.8	11/42.3	2/7.7	2/7.7	2/7.7	—	26
Complex C	4/16.7	4/16.7	5/20.8	3/12.5	7/29.2	1/4.2	—	—	24
Complex D	2/9.5	6/28.6	2/9.5	3/14.3	1/4.8	7/33.3	—	—	21
I total	10/14.1	14/19.7	8/11.3	17/23.9	10/14.1	10/14.1	2/2.8	—	71
				Lo Demás—Sector IV					
26D total	3/25.0	1/8.3	1/8.3	3/25.0	1/8.3	2/16.7	1/8.3	—	12
				Lo Demás—Sectors I and IV combined					
Total	13/15.7	15/18.1	9/10.8	20/24.1	1/13.3	12/14.5	3/3.6	—	83
				Huacarones					
Total	22/20.4	14/13.0	22/20.4	17/15.7	1/0.9	28/25.9	2/1.9	2/1.9	108

(1987:208–209): storage, transformation or processing (cooking), and transfer or transport (serving and eating).

Comparison of the total Lo Demás sample of shape-assigned sherds with that from Huacarones (Table 7) reveals some interesting patterns, particularly concerning the shape categories for which use inferences are strongest. The primary cooking vessel from Lo Demás, the angular rim bowl, has a similar frequency at the two sites (15.7% at Lo Demás, 20.4% at Huacarones). The secondary Lo Demás cooking vessel shape, the constricted bowl, is more common at Lo Demás than at Huacarones, as are restricted jars, a form which seems to have served multiple purposes (*see* Table 7). The two assemblages differ most significantly in two shape categories: wide-mouthed jars and bottles. Wide-mouthed jars are about twice as common at Huacarones as at Lo Demás (20.4% vs. 10.8%); these vessels were almost certainly used for dry storage, particularly the Huacarones variant with labial flanges. The wide-mouthed jars are particularly suited for storing agricultural produce. In this context, it is important to recall that the unsooted wide-mouthed jar sherds—especially those with labial flanges—are the thickest rim sherds in the ceramic assemblages from either site.

In contrast, bottles account for over 10% of the Lo Demás shape-assigned rim sherds but are almost absent at Huacarones (Table 7). Bottles were probably used to hold liquid, possibly of greater importance in a non-agricultural settlement located away from irrigation canals and other sources of potable water than at a valley floor farming site such as Huacarones. Use of gourds for liquid containment might have been more common at the farming site, but the data from Lo Demás show that the fishermen had access to gourds and may even have grown them (*see* Chapters 8 and 10).

CHRONOLOGY AND CULTURAL AFFILIATION

The analysis of vessel forms from the Lo Demás ceramic assemblage offers limited information concerning chronology and affiliation. One angular rim bowl sherd (Fig. 20h) from the basal stratigraphic complex (B) in Sector I resembles a Late Horizon Ica 9 form which Menzel (1966) found in the Uhle Chincha collection. Angular rim bowls in general (Fig. 20) are found in "ordinary Late Horizon refuse sites in Ica" (Menzel, 1976:44), but they also seem related to a small cooking olla found in a Cemetery B Chincha grave in association with a possibly pre-LIP 8 bottle/jar (Menzel, 1966), and to a Late Intermediate Period form from Cerro Azul, in the neighboring Cañete valley (Marcus, 1987*b*). These associations suggest that this shape is a conservative, pre-Inka form which was in use for a long time.[60] A number of restricted jar necks are also similar to those on Menzel's (1966) LIP 8/early LH Chincha style ovoid jars (Fig. 23e, g–k); most of these sherds come from Complex B, the basal complex.

The decorated sherds from Lo Demás provide more information on chronology and cultural affiliation than do the undecorated rim sherds.

Decoration

Like shape-diagnostic sherds, decorated fragments from Lo Demás are too few and fragmentary

Table 8.—*Decorated body sherds from Lo Demás illustrated in Figs. 29–32. Abbreviations: Fig., figure reference for this monograph; Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex in Sector I; Su, Subunit; L/F, level or feature within excavation unit; b, beige; br, brown; cr, cream; dp, dark purple; g, grey; o, orange; r, red; s, slip; ext, exterior; int, interior; td, throat diameter. Sherds are unsooted unless otherwise noted; decoration is painted on the exterior unless otherwise noted.*

Fig.	Cat.	SC	Su	L/F	Paste	Surface	Other
				Sector I			
29a	1578	B	3A	12	r-o	ext cr s	13 cm td
29b	1741	B	2C	19	r-o	ext r s	16 cm td
29c	1389	B	10B	23	g-o	o	
29d	1760	B	4B	20	o	ext cr s	
29e	1657	B	2A	14b	r-o	r-o	
29f	1855	B	4B	25	o	ext cr s	
29g	1324	B	10D	20i	g ext	ext r s	
29h	1324	B	10D	20i	g ext	ext r s	
29i	1391	B	10D	24	r-o	ext r s	
29j	1843	B	4B	II408	r-o	r-o	
29k	1193	B	1C	26W	r-o	r-o	
29l	1834	B	4B	23i	g ext	ext r s	
29m	1391	B	10D	24	r-o	ext r s	
29n	1850	B	4D	25	b	b	
29o	1909	B	C-I	13	r-o	ext r s	
29p	1278	B	3B	9	g core	br	
29q	1819	B	4D	22i	r-o	ext r s	
29r	1910	B	C-I	14	r-o	ext r s	
29s	1172	B	1C	22W	r-o	r-o	
29t	1669	B	2A	14ci	r-o	r-o	
29u	1844	B	4B	II49	r-o	ext dp s	
29v	1327	B	10D	1023	r-o	ext r s	
29w	1502	B	3B	10	br-b	b	int decoration
29x	1857	B	4D	II412	g	g	incised
30a	1684	C	2C	291	r-o	ext cr s	12 cm td
30b	1598	C	4D	465	r-o	r-o	
30c	52	C	A2	3bii	r-o	r-o	
30d	904	C	3D	6b	r-o	ext r s	
30e	412	C	1B	111	r-o	r-o	
30f	412	C	1B	111	r-o	r-o	
30g	52	C	A2	3bii	r-o	o	ext soot
30h	52	C	A2	3bii	r-o	o	ext soot
30i	52	C	A2	3bii	r-o	r-o	int soot
30j	1396	C	3A	336	r-o	r-o	
30k	957	C	3B	6c	o	ext r s	
30l	1428	C	2C	278	r-o	ext cr s	
30m	484	C	3A	311	g core	b	
30n	882	C	1A	16iW	r-o	ext r s	
31a	1085	D	4D	450	b	b	
31b	90	D	A3	f23	r-o	r-o	
31c	1134	D	4C	7c	r-o	r-o	
31d	1134	D	4C	7c	r-o	o	
31e	387	D	2D	3d	o	o	
31f	1134	D	4C	7c	r-o	r-o	
31g	31	D	B3	2a	r-o	r-o	
31h	19	D	A2	2d	g-o	g-o	
31i	783	D	4B	5	r-o	ext cr s	
31j	554	D	2C	2W	b	o	
31k	662	D	2C	3bW	r-br	r-br	
31l	1106	D	4C	7b	r-o	ext cr s	
31m	240	D	1A	1	r-o	r-o	
31n	554	D	2C	2W	b	o	
31o	295	D	2B	2	g	g	broken handle bases; modelled potato eye

Table 8.—*Continued.*

Fig.	Cat.	SC	Su	L/F	Paste	Surface	Other
31p	392	D	2D	202	g	g	modelled potato eye; oval protuberances
31q	299	D	1D	4E	g	g	lug w/incisions; int soot
31r	291	D	1D	2ibE	g	g	incised; int soot
				Sector IV			
32a	1858		26D	16	r-br	ext r s	8 cm td
32b	1841		26D	13	g core	g-o	9 cm td
32c	1800		26D	10	r-o	g	handle; sooted
32d	1851		26D	13b	r-o	r-o	
32e	1809		26D	12	r-o	r-o	
32f	1874		26D	17	r-o	ext r s	sherd worked into rough disk
32g	1717		26D	3	r-o	r-o	
32h	1745		26D	6b	b	ext r s	
32i	1681		26D	2	g core	ext cr s	
32j	1681		26D	2	r-o	ext r s	
32k	1853		26D	14b	o	ext cr s	
32l	1800		26D	10	r-o	ext cr s	
32m	1874		26D	17	r-o	r-o	
32n	1800		26D	10	r-o	r-o	ext soot
32o	1852		26D	13bi	r-o	ext cr s	
32p	1800		26D	10	r-o	r-o	incised; ext soot

to create a typology. Instead, diagnostic designs from the Lo Demás sherds are correlated with published ceramic decoration from Chincha and elsewhere.[61]

Lo Demás ceramics employ three decorative techniques. Most decorated sherds are painted; a few examples are modeled and/or incised. The following sections are organized by decorative technique. Table 8 lists attributes of the decorated body sherds, which are illustrated in Figs. 29–32. Decorated rim sherd attributes are listed in Table 6.

Painted decoration.—Menzel (1966:89–94) describes but does not illustrate decoration on the Uhle Chincha collection ceramics of her LIP 8/early LH Chincha style and makes passing reference to decoration on the pottery included in her post-Chincha assemblage (Menzel, 1966:109–118 *passim,* 118–119), but does refer to Kroeber and Strong's (1924) illustrations. Menzel's (1976) well-illustrated study of contemporary Ica decoration provides some comparative material, as do various other studies of late pre-Hispanic Peruvian pottery.

Painted designs from Lo Demás are exclusively geometric; a small number represent geometricized fish and the rest consist of abstract figures. Painting occurs exclusively on oxidized-fired vessels. Figures tend to be drawn in black or dark brown[62] on a paste-colored or cream-slipped background; white and red are often used to separate the dark lines and are occasionally used as background slips. Dark purple is used rarely in place of black or dark brown to form the figures.

Most painted fragments from Lo Demás are body sherds, so relating design to form is usually not possible. However, three categories of decorated sherds have characteristic associations between design and form: (1) rims with the Chincha Rim Scallop, (2) shoulder/neck fragments with outlining at the base of the neck, and (3) plates with a striped design on the interior. In addition, two unique sherds—a handle and an open bowl rim—link elements of painted decoration and form.

(1) The Chincha Rim Scallop. Menzel (1976: 135) describes this design element as "a row of adjoining small solid black triangles on a white or unpigmented surface, pendent from the rim edge" (*see also* Menzel, 1966:92, 1976:117, 146). On the six Lo Demás examples (Table 6), at least, the lip is also painted solidly in the same color as the triangles. Five have dark brown paint for the design (Figs. 23f, r, s, 25a, j) and one uses black paint (Fig. 23p). Four of the sherds are rims classified as restricted jars and two as bottles (*see above*). Examples come from Stratigraphic Complexes B to D in Sector I and from Subunit 26D in Sector IV, indicating that this design feature was used throughout the late pre-Hispanic occupation of Lo Demás.

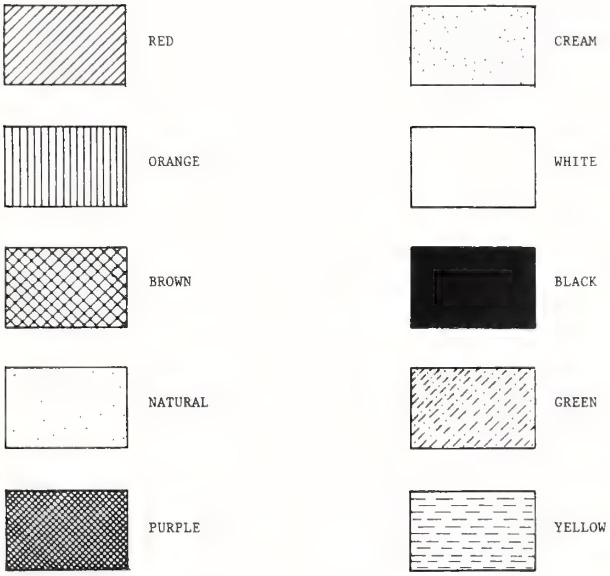

Fig. 28.—Color key for sherd drawings.

Menzel (1966:92) writes that for her LIP 8/early LH Chincha style, "jar necks are almost invariably decorated with" the Chincha Rim Scallop. This design element is not cited in the later LH post-Chincha assemblage pottery, and it is not present on pre-LIP 8 Chincha ceramics (D. Menzel, personal communication, 1987).

In Ica pottery, the Chincha Rim Scallop first appears on LIP 8 Ica 8 vessels, where it "must be the result of Chincha influence" (Menzel, 1976:117), and continues in use in LH Ica 9 pottery; but

> "Since most Chincha-associated features are eliminated in the Late Horizon, the survival of the Rim Scallop design requires special explanation. It probably owes its survival to the fact that it has a coincidental close analogue in the Cuzco Inca style, where rows of pendent black triangles are used for various purposes, including interior (upper) rim decoration" (Menzel, 1976:135).

However,

> "The Chincha Rim Scallop differs from the similar Inca rim in context, and also in execution, the triangles having a proportionately broader base with a less pointed tip, slightly arching sides and more irregular contours" (Menzel, 1976:146).

The examples of the Chincha Rim Scallop from Lo Demás fit the description for the Chincha (vs. Inka) variant best; however, this design is still best explained as an example of Inka influence on Chincha pottery (*see below*).

Two Chincha Rim Scallop sherds from Sector I of Lo Demás (Figs. 23p, 25j) were found in the same stratigraphic complex (B, the lowest) as a sherd bearing a Cuzco Inka Polychrome A design (Fig. 29c) (*see below* and Rowe, 1944:47 and Plate V); two other Rim Scallop sherds were found in later, overlying Complexes C (Fig. 23f) and D (Fig. 25a). In Subunit 26D in Sector IV, the two Chincha Rim Scallop sherds (Fig. 23r, s) were stratigraphically lower than the Inka plate fragment (Fig. 27c; *see below*). These data indicate that although the Chincha Rim Scallop *might* precede the Inka arrival in Chincha, it certainly continued in use during the Inka occupation (as Menzel [1976] shows for Ica). Therefore, the Chincha Rim Scallop could well be a design feature inspired by Inka ceramic decoration, *contra* Menzel. The fact that this design element does not appear in Chincha or Ica before LIP 8, as well as the presence of Late Horizon, Inka-related stylistic attributes on some figurine and anthropomorphically-modeled pottery fragments from Lo Demás (*see* Chapter 8) further support this hypothesis (*see below* and Chapter 11).

(2) DECORATED SHOULDER/NECK FRAGMENTS WITH THE CORNER POINT PRESERVED BUT LACKING THE RIM AND MOST OF THE NECK. Decoration on these sherds consists of neck outlining and is present on six fragments (Figs. 29a, b, 30a, b, 32a, b); a seventh probably broke just below the corner point (Fig. 31a). Throat diameter, where measurable, ranges from 8 to 16 cm, indicating that the vessels probably fall into the "restricted jar" shape category. Examples of decorated shoulder/neck sherds occur in Subunit 26D in Sector IV and in Stratigraphic Complexes B and C in Sector I. The seventh, probable example comes from Stratigraphic Complex D; thus, this design feature seems constant throughout the late pre-Hispanic occupation of Lo Demás. Two of the restricted jar neck sherds with the Chincha Rim Scallop found in the quebrada adjacent to Sector IV of Lo Demás also have neck outlining (Fig. 24a, b).

All but one of the decorated shoulder/neck sherds have a red or cream slip and two or three narrow, black or dark brown lines circling the shoulder of the vessel at and/or just below the corner point. The exception has a broader cream band around the top of the shoulder, joined by a diagonal cream band which strikes across the shoulder (Fig. 32b). The cream design is painted over a brown slip.

Menzel's (1966:91–92) description of the following Chincha style design feature is relevant to the decorated shoulder/neck fragments from Lo Demás (except the cream band sherd):

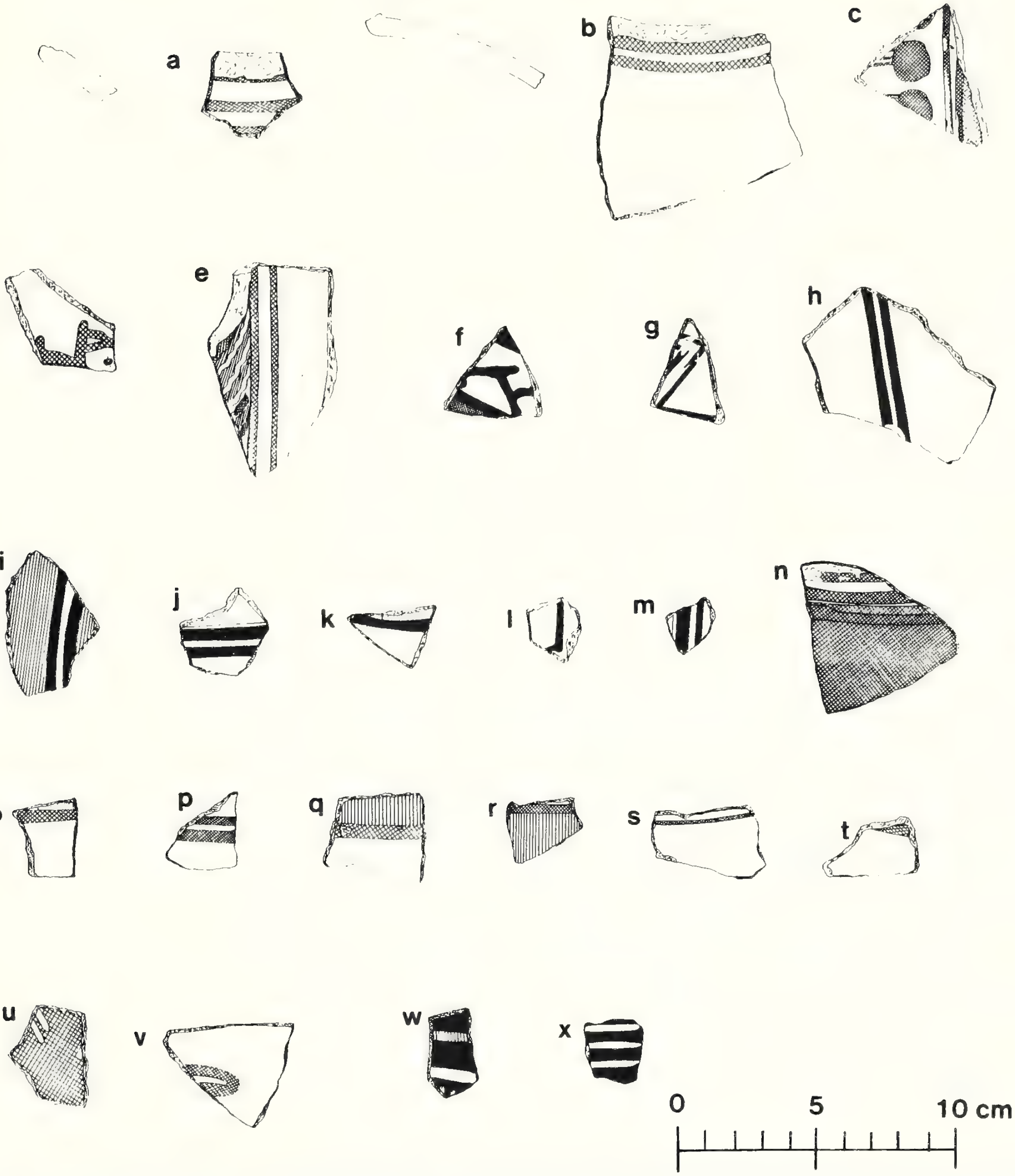

Fig. 29.—Decorated body sherds from Lo Demás, Sector I, Stratigraphic Complex B. See text and Table 8 for further information. See Fig. 28 for color key.

> "The design area is located on the upper exterior part of the body. . . . The design area may or may not be delimited at the bottom by an outline which is placed at or above the shoulder of the vessel. Outlining consists of a single black line, two or three black lines, or a purple or red band outlined in black."

Menzel does not indicate whether this kind of outlining is used to delimit the *top* of the design area, although such appears to be the case on a number of the Chincha vessels illustrated by Kroeber and Strong (1924:Plates 11a–d, 12a, b). Two of these vessels (Kroeber and Strong, 1924:Plate 12a, b) are jars identified as Chincha Ica by Menzel (1966:93 and Appendix A) on the basis of their decoration. The other four vessels are complex rim bowls, three

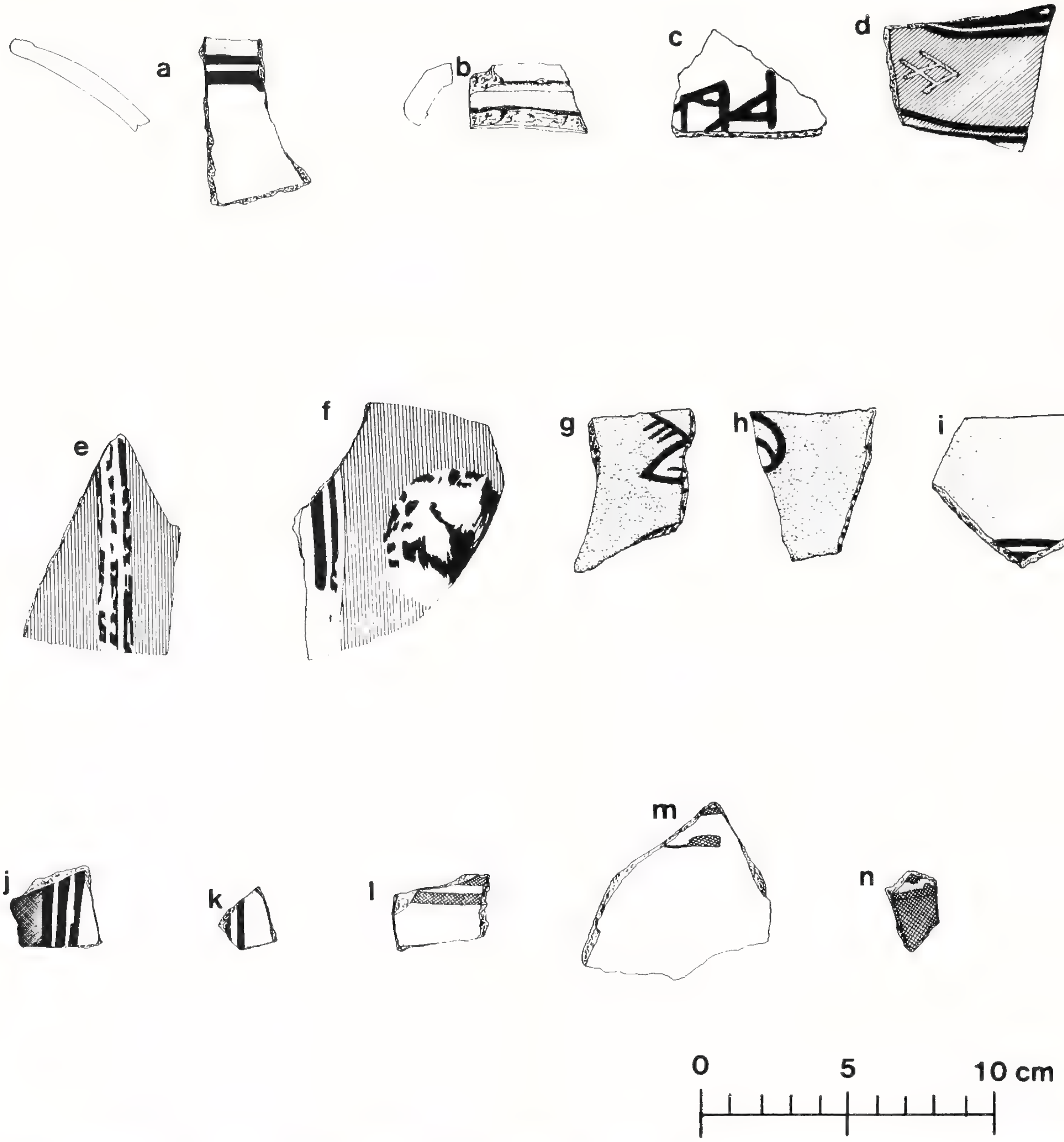

Fig. 30.—Decorated body sherds from Lo Demás, Sector I, Stratigraphic Complex C. See text and Table 8 for further information. See Fig. 28 for color key.

with Chincha Ica decoration (Kroeber and Strong, 1924:Plate 11a, b, d; Menzel, 1966:93 and Appendix A) and one with Chincha decoration (Kroeber and Strong, 1924:Plate 11c; Menzel, 1966:92 and Appendix A). Based on the shoulder angle, the jars provide a closer analogue for the Lo Demás shoulder/neck sherds than do the complex rim bowls.

Menzel (1966:92–93 and Appendix A) assigns the two jars and the four bowls to her LIP 8/early LH Chincha style chronological unit. However, she does not provide sufficient information to determine whether or not shoulder/neck outlining also occurs on post-Chincha assemblage pottery. In Ica, the apparent source for this decorative technique, a review of the photos published by Menzel (1976) shows that shoulder/neck outlining occurs on vessels assigned to the Late Horizon and the early Colonial Period.

(3) Interior-decorated Plate Sherds (Fig. 27a, b). Two sherds come from Stratigraphic Complex B, the lowest complex in Sector I. Decoration consists of painted red and white stripes with black outlines running perpendicular to the rim on the interior of the vessel; the exterior is not painted.

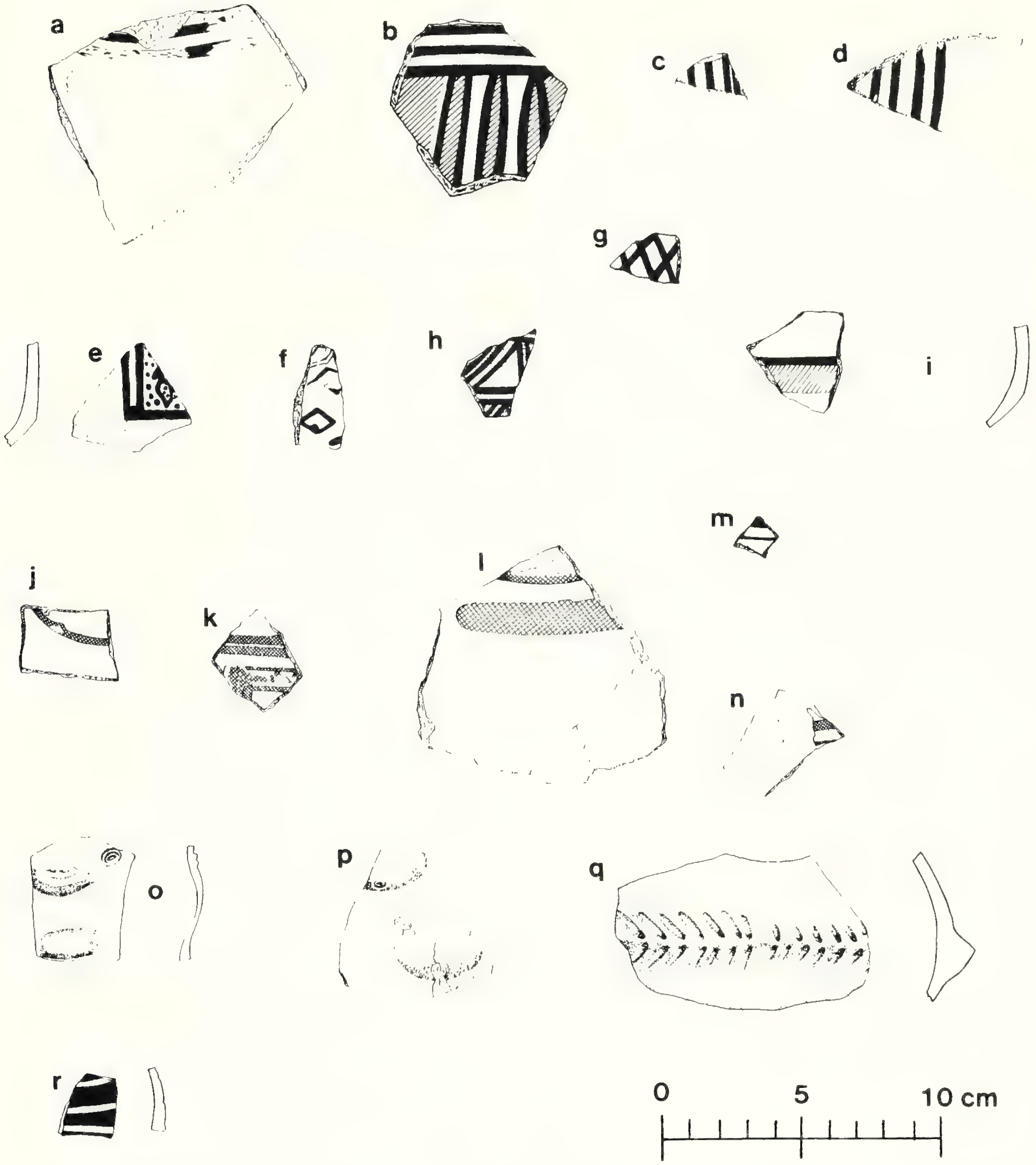

Fig. 31.—Decorated body sherds from Lo Demás, Sector I, Stratigraphic Complex D. See text and Table 8 for further information. See Fig. 28 for color key.

The red/white/black outline stripe design is noted by Menzel (1976:106, 144–145) for LIP Ica 6 and LH Ica 9, but not mentioned for Chincha (Menzel, 1966). On one Ica 9, Late Horizon "flaring cup" (Menzel, 1976:Plate 53–48), both horizontal and vertical variants of this stripe pattern are among several designs which alternate around the interior of the rim. The shape of the deeper Lo Demás striped rim (Fig. 27b) could be interpreted as part of a flaring cup rather than as a dish.

Three body sherds from Stratigraphic Complex D in Sector I of Lo Demás have a red/white/black outline design similar to that on the two plate rims (Fig. 31b–d). Unfortunately, the position of these fragments on the original vessels cannot be determined.

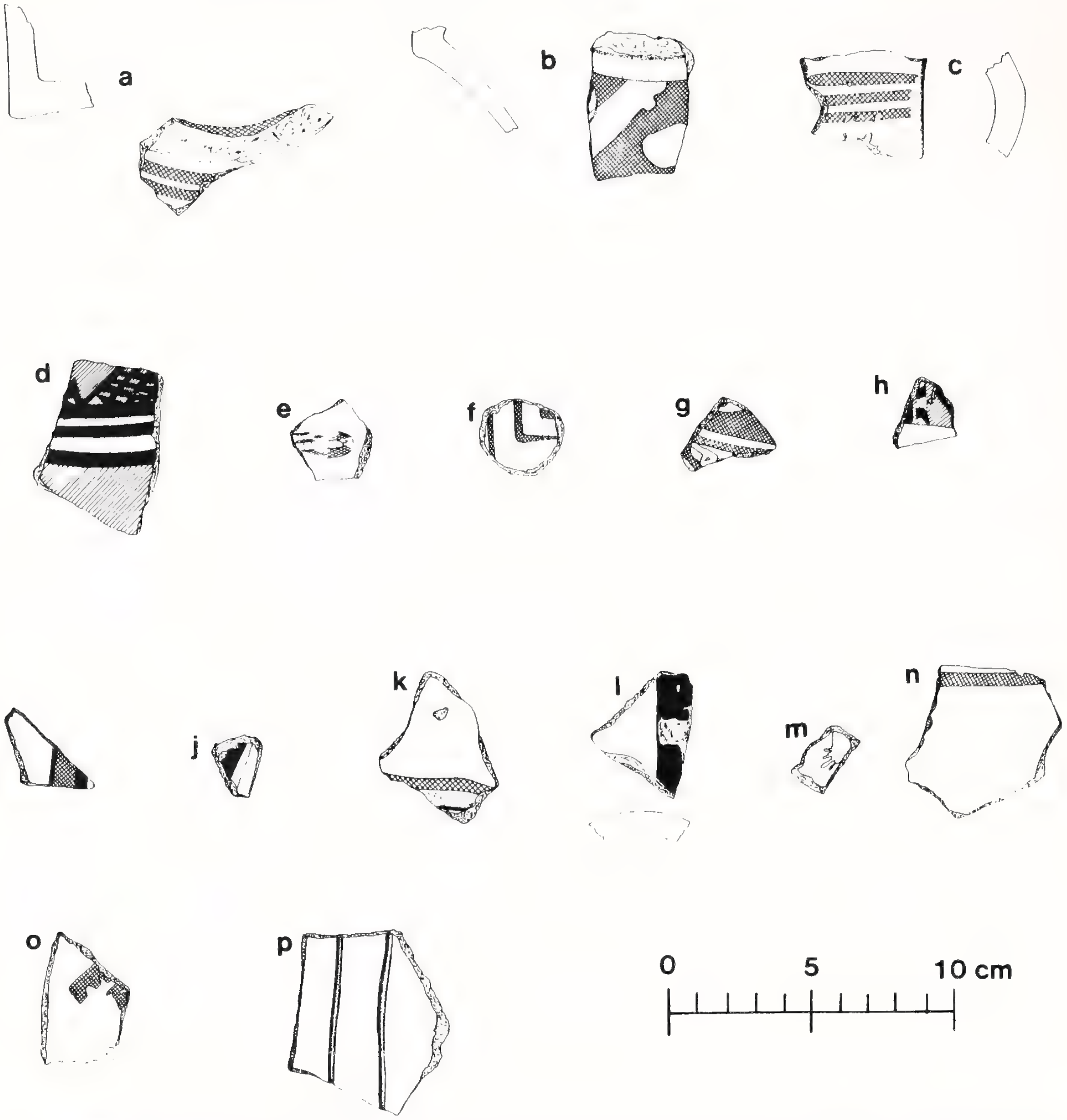

Fig. 32.—Decorated body sherds from Lo Demás, Sector IV, Subunit 26D. See text and Table 8 for further information. See Fig. 28 for color key.

The Lo Demás ceramic assemblage from Subunit 26D in Sector IV includes one strap handle fragment with a painted design consisting of three dark brown stripes running from edge to edge of the handle (Fig. 32c). The paste is red-orange, tending toward grey on the surface, which is sooted. Concerning LIP 8/early LH Chincha style decoration, Menzel (1966: 92) writes that

> "handles are decorated with cross striping. The cross striping consists of the same designs as the basal outlining of the design areas."

Although Menzel does not mention striped handles on vessels in the post-Chincha assemblage, one of the post-Chincha pots illustrated by Kroeber and Strong (1924:23, Fig. 9d) has a cross-striped strap handle. Menzel (1966:113) classifies this fruit-shaped vessel as a Late Horizon, central to north coast specimen. Strap handles, sometimes decorated with cross-striping, are a characteristic design feature of Inka pottery; this feature was employed in Ica in the Late Horizon Ica Inka style (Menzel, 1976:136, 156).

Stratigraphic Complex C in Sector I of Lo Demás provided a open bowl rim (Fig. 26h) with dark brown, linear elements painted over a cream slip on the exterior of the vessel. The preserved design on this sherd is too fragmentary and simple to allow cross-correlation with other designs. However, cream slips are one of the characteristic design features of Menzel's (1966:91) Chincha style.

In addition to the painted sherds that preserve the relation of design to form, the Lo Demás ceramic assemblage includes a number of painted fragments which show some similarity to Chincha, Ica, and Inka designs.

Two sherds have clear Inka decoration, though it is less obvious whether they represent imported Cuzco pottery or local imitations. The first is a body sherd with Cuzco Polychrome A decoration (Rowe, 1944:47 and Plate V) in dark brown on an unslipped, orange surface (Fig. 29c). The paste is a grey-orange color. One of the design elements of Cuzco Polychrome A is the "fern" pattern, which consists of balls attached by two or three lateral stems to central stems. The Lo Demás sherd preserves one whole and two partial balls; the whole ball has three lateral stems. Sherds exhibiting the fern pattern are reported from almost every published provincial Inka site (e.g., Julien, 1983:Plate 25; Morris and Thompson, 1985:75, Fig. 9).[63]

The other Inka sherd is a rim fragment of a plate found in Subunit 26D in Sector IV (Fig. 27c; *see above,* section on plates/dishes). Decoration consists of an interior design of black and white lines separating areas of brown and weak red and a black rim scallop on a white base; the rim scallop is reminiscent of Menzel's (1976:135, 146) Chincha variant rather more than her Inka variant. The colors are brighter and the outlines sharper than on most of the decorated sherds from Lo Demás. Brian Bauer (personal communication, 1988) has identified this sherd as part of an Inka plate, based on his research in the Cuzco area.

Geometric fish occur on two sherds in Stratigraphic Complex C in Sector I, and on one sherd in Complex B. The Complex B fish (Fig. 29d) is the same type as one of the Complex C fish (Fig. 30c); the former is in dark brown on a cream surface, whereas the latter is black on orange paste. Bird figures but not fish are listed as an element of Chincha style decoration (Menzel, 1966:92). Geometric fish do appear on two Chincha vessels illustrated by Kroeber and Strong (1924:Fig. 6a, b), but they are not the same fish as either of the two Lo Demás types.[64] Rather, the Lo Demás fish are identical to the Late Horizon, Ica–Inka rectangle fish (Menzel, 1976:164 and Plate 36–493). A bottle sherd from the Sector IV quebrada surface collection (Fig. 24d) has a very similar fish and the Chincha Rim Scallop.

The second type of geometricized fish occurs on one fragment from Stratigraphic Complex C in Sector I (Fig. 30d). This fish is executed in cream on a red-slipped background; the design field is set off by black lines over the red slip on one side and over cream on the other. These lines fit Menzel's (1966: 91–92) description of Chincha style design area outlining, as cited above. Although fish of this form are not seen on published illustrations of vessels from Ica (Menzel, 1976) or Chincha (Kroeber and Strong, 1924), the Lo Demás fish is closely similar to fish on a warp-patterned camelid fiber belt from Uhle's (1924) Cemetery E, Grave 3 (*see* Garaventa, 1979: 220, 225, Figs. 8, 231); except that the former lacks the central dot eye of the textile fish. The form of this design is constrained by the technical limitations of the textile medium (unlike the painted rectangle fish), so it probably originated as a textile design (M. Young, personal communication, 1988). Menzel (1966) places Grave E–3 in her LIP 8/early LH Chincha style. Based on the presence of several silver goblets and an analogy to an Ica grave, Garaventa (1979:224) suggests that Grave E–3 may date to the early LH part of the Chincha style.

Two sherds from Stratigraphic Complex D in Sector I of Lo Demás somewhat resemble early Colonial Period Ica 10 designs. The first is done in black on an even cream slip; the design consists of part of a box containing black dots and a curvilinear figure (Fig. 31e). This design is very similar to one on an Ica 10 fragment from refuse (Menzel, 1976:Plate 43–597). The second example is an orange paste, unslipped sherd with small diamonds painted in fugitive black (Fig. 31f), which resembles Menzel's Ica 10 (early Colonial Period) small diamond element (Menzel, 1976:Plates 40–565, 567, 570, 574 left).

Another sherd from Complex D (Fig. 31g) has part of a black on red-orange paste cross-hatched design somewhat similar to Late Horizon, Inka-associated designs from Ica (Menzel, 1976:Plates 34–448, 457). A fourth sherd from Complex D (Fig. 31h) vaguely resembles a design feature found on "Canchón" pottery from Cuzco (Rowe, 1944:Figs. 19–13, 17, 18) comprised of triangles formed by multiple black lines.

A Complex B sherd with a red, white, and dark brown on cream design (Fig. 29e) strongly resembles a Chincha Ica style design from Uhle's Cemetery E in Chincha (Kroeber and Strong, 1924:Plate 11a; Menzel, 1966:93 and Appendix A). The Cemetery E vessel is a cambered-rim bowl assigned (Menzel, 1966:86–87) to the LIP 8/early LH Chincha style chronological unit. The design on the Lo Demás sherd consists of red, dark brown, and white wavy lines set diagonally to two dark brown lines on a cream background.

A sherd from Subunit 26D in Sector IV of Lo Demás (Fig. 32d) is similar to a Provincial Inka plate design from the Ica valley (Menzel, 1976:51–39). The Lo Demás fragment has black triangles with interior cross-hatching over a red slip; the base of the triangle rests on the first of three black lines separated by cream bands. On the opposite side of the black/cream bands is a red or light brown field. In the Provincial Inka design, the triangles are not joined, there are only two black bands, and the background color is different. A variety of other designs from Ica have cross-hatched triangles; all date to the Late Horizon (Menzel, 1976:Plates 34–442, 460, 461, 35–469).

The Lo Demás ceramic assemblage contains a number of other painted sherds (Figs. 29f–w, 30e–n, 31i–n, 32e–o). Most bear a generic relationship to Chincha style decoration (Menzel, 1966), but none have a striking resemblance to any published specimens.

Modeled decoration.—Some sherds from Lo Demás have modeled decoration which seems related to various published late pre-Hispanic coastal styles. Most conspicuous are several fragments with anthropomorphic features; these specimens, which are very similar to Late Horizon pieces from Pachacamac, are discussed in Chapter 8 in conjunction with the ceramic figurines. Three other sherds, all from Stratigraphic Complex D in Sector I, are discussed here.

Two blackware sherds from approximately equivalent proveniences in Subunits 2B and 2D appear to be part of a vessel representing a tuber (Fig. 31o, p). One of the sherds has the base for a strap handle (Fig. 31o); both are relatively thin, with irregular profiles composed of molded bumps which imitate the surface of a tuber. Each sherd has a circular appliqué feature resembling a potato eye. Fruit and tuber vessels are relatively common in the Uhle Chincha collection. Menzel (1966:113–115) considers these pots as representatives of central to north coast, Late Horizon styles and assigns them to her post-Chincha assemblage. One illustrated vessel (Menzel, 1966:114 and Plate XVI–73) represents a potato through a series of bumps like those on the Lo Demás sherds. This pot and all of the other fruit and tuber vessels in the Uhle collection are oxidized-fired, but a nearly identical potato pot from Pachacamac is made of smoked blackware like the Lo Demás example (Menzel, 1966:114).

Another blackware sherd from Complex D has a long, raised lug with symmetrical, angled incisions along both sides of the crest (Fig. 31q). The Uhle collection from Chincha contains two blackware vessels with appliqué maize ear lugs which Menzel (1966:97 and Plates XI–24, XII–31) assigns to her LIP 8/early LH Chincha style. However, the resemblance between these lugs and the Lo Demás sherd is slight.

Incised decoration.—In addition to the possible maize ear lug discussed in the preceding paragraph, the Lo Demás ceramic assemblage contains three other incised body sherds, three of blackware and one of oxidized-fired, red-orange paste, and an incised blackware handle fragment. The blackware body sherds, from Stratigraphic Complexes B and D in Sector I, consist simply of small fragments with parallel incised lines (Figs. 29x, 31r). Although blackware vessels compose nearly half of the vessels in the Uhle collection assigned by Menzel (1966:89) to her Chincha style, apparently none of these vessels is incised except for the details on the maize ear lugs and on the handles of one bottle. In contrast, blackware vessels in a number of styles assigned to the post-Chincha assemblage do have incised decoration (e.g., an imitation Ica 9 pot, Menzel, 1966: 116; four Chincha Inca bowls, Menzel, 1966:117, Kroeber and Strong, 1924:Plate 13a–c; a Pachacamac Inka bottle, Menzel, 1966:112, Kroeber and Strong, 1924:13, Fig. 3b).[65]

The blackware handle from Stratigraphic Complex D in Subunit A1 is solid, tubular (18 mm diameter), and curved. The incisions run diagonally to the long axis of the handle. This sherd strongly resembles the vertical fillet handle on a Pachacamac Inka blackware bottle from Uhle's Site E (Menzel, 1966:112 and Plate XV–64; Kroeber and Strong, 1924:13, Fig. 3b), and has a lesser resemblance to handles on a Chincha style blackware bottle from Uhle's Site C (Menzel, 1966:Plate XI–21). Concerning the Pachacamac Inka vessel, Menzel (1966: 112) writes that "the use of the fillet is a coastal modification" to an Inka shape, Rowe's (1944:48, Fig. 8d) Shape D, which has strap handles instead of the tubular fillet handles. Also, the coastal bottles have appliqué neck bands (often incised as on the

Uhle bottle), "an original coastal feature found on late period vessels from Pachacamac to the north coast" (Menzel, 1966:112).

The incisions on the oxidized-fired sherd from Subunit 26D in Sector IV (Fig. 32p) are also parallel. Menzel (1966) does not mention any incised oxidized vessels in the Uhle collection.

Conclusions: Chronology and Cultural Affiliation from Decorated Ceramics

The decorated sherds from Lo Demás provide somewhat more information concerning chronology and cultural affiliation than do the rim sherds. The clearest indicators are the sherds in the Inka style found both in the lowest stratigraphic complex in Sector I (Fig. 29c) and in level 26–5 in Subunit 26D, Sector IV (Fig. 27c). Another sherd, from level 26–13b in Subunit 26D, also appears to bear an Inka design.

In addition to the Inka Polychrome A sherd, Complex B in Sector I has sherds which seem related to Late Horizon styles from Ica, to the south (Figs. 27a, b, 29d), and Pachacamac, to the north (Fig. 36), and to an LIP 8/early LH Ica style (Menzel's [1966:102–105] Chincha Ica variant of her Chincha style). Complex C also has probable Chincha Ica pottery (Fig. 30a, b), along with a Late Horizon Ica–Inka design (Fig. 30c) and an early Late Horizon Chincha design (Fig. 30d). Complex D contains sherds related to several Late Horizon styles: Ica Inka (Fig. 31g), Cuzco Inka (?) (Fig. 31h), and Pachacamac Inka (Figs. 31o, p, 36). Two sherds from Complex D seem most closely related to Menzel's (1976) early Colonial Ica 10 style (Fig. 31e, f).

In Sector IV, level 26–16 of Subunit 26D (near the bottom of the excavation) had one sherd with shoulder/neck outlining, possibly a Chincha Ica feature (Fig. 32a). Level 26–13b contained a sherd with decoration resembling a Provincial Inka plate from Ica (Fig. 32d). A striped strap handle from level 26–10 probably represents a Chincha style feature, although there are also Late Horizon, Ica Inka variants of this design. Finally, the Inka plate fragment came from level 26–5.

All three major complexes in Sector I, as well as Subunit 26D in Sector IV, contained sherds with the Chincha Rim Scallop design (Figs. 23f, p, r, s, 25a, j). Menzel (1966, 1976) considers this design to be a purely Chincha element uninfluenced by similar pendent triangles in the Inka pottery tradition. However, the Chincha Rim Scallop is one of the few designs which survive from LIP 8 Ica 8 into LH Ica 9 in the Ica valley (Menzel, 1976), and the stratigraphic distribution of this feature in Lo Demás suggests that it could well be the result of Inka influence in the Late Horizon (especially considering that it does not appear on pre-LIP 8, pre-Chincha style ceramics).

The decorated ceramics from Lo Demás are eclectic, but they point quite clearly to the co-existence of features which Menzel (1966:79) considers to belong to two chronologically distinct units: the LIP 8/early LH Chincha style and the later LH post-Chincha assemblage.

Menzel (1966:97) writes that "the Chincha style cannot have persisted very long in the Late Horizon, and must be confined to its beginning years" (*see also* Menzel, 1967:23; Menzel and Rowe, 1966:64–65 and Plate VIII). Although it is probable that at least some of the Chincha design elements do antedate the Inka conquest of the Chincha valley, the stratigraphic evidence from Lo Demás makes it equally clear that the Chincha style did not terminate with—or probably at any time during—the Inka governance of the valley. Based on his work at La Centinela and other Chincha sites, C. Morris (personal communication cited by Netherly, 1988*a*:112) also believes that the Chincha style continued in use throughout the Late Horizon. The fact that many of the burials excavated by Uhle contained only items datable to the Late Horizon and did not contain Chincha style items can now be explained more parsimoniously by social, political, or occupational differences. Menzel (1966:121) proposes this explanation for the heterogeneous collection of pottery in her post-Chincha assemblage unit of association; the Lo Demás evidence indicates that Menzel's Chincha style unit of association should be covered by the same hypothesis. This solution explains the presence of occasional Late Horizon elements in burials classified by Menzel as Chincha style, as well as the presence of some Chincha elements (e.g., a Chincha style figurine, Menzel, 1967:23) in post-Chincha burials.

One consequence of this reinterpretation of the late pre-Hispanic Chincha pottery sequence is that the presence of Chincha style pottery does not necessarily indicate a pre-Inka date. A second consequence is that the Ica 9 style no longer needs to appear in Chincha earlier than in Ica, as Menzel (1966:96) suggests.

The chronology and cultural affiliations of Lo Demás are considered further in Chapters 8 and 11.

CHAPTER 8

ARTIFACTS OTHER THAN CERAMIC VESSELS

This chapter treats all of the artifact categories from Lo Demás except pottery vessels, which were discussed in Chapter 7. Artifacts are defined here as items manufactured or deliberately modified by the prehistoric inhabitants of the site. Categories covered in the following sections are: figurines; metal objects; wooden objects; worked gourd; nets; textiles; spinning and sewing equipment (spindle whorls, needles, and spindles); sandal; "half-bobbin" objects; lithics; and bone and shell objects. Unless otherwise noted, the samples discussed for each artifact category consist of all specimens from all excavations in Sector I[66] and from Subunit 26D in Sector IV. These artifacts help determine the activities carried out at Lo Demás and the chronology and cultural affinities of the site.

FIGURINES

Figurines, or modeled representations of the human figure, occur in Peruvian archaeological sites spanning thousands of years of prehistory. The earliest known figurines in Peru date to the Late Preceramic Period (Feldman, 1980:148–156), and examples are found in sites from every subsequent period through the Late Horizon.

For the late pre-Hispanic periods of the south coast, Menzel (1967) has studied and cross-dated collections of clay figurines from Ica, Chincha, and several other areas. She identified a style of unbaked clay figurines from a cache in Ica dating to Ica 6 (= Late Intermediate Period Epoch 6), but could not point to any similar examples from elsewhere. For Late Intermediate Period Epoch 8 and the early Late Horizon, however, Menzel defined a Chincha style of fired clay figurines separate from a wide-spread south coast style of Late Horizon figurines showing Inka influence. The LIP 8 Chincha style includes several variants: adult female (most common), juvenile female, and infant. The Late Horizon south coast style has only adult females. The figurine fragments from Lo Demás are related to the Chincha and south coast LH styles.

Three figurine fragments were recovered in Sector I and three fragments in Sector IV. Sherds from two pottery vessels with anthropomorphic modelling were also found in Sector I.

Sector I Figurines and Related Pieces

The three figurine fragments from Sector I came from two different contexts, both in Stratigraphic Complex C. A complete head, broken at the neck, was found face up in Subunit 3B (Fig. 33). This head shows most of the characteristics of Menzel's LIP 8/early Late Horizon Chincha style, adult female variant: solid clay fired to a tan-orange color, a squared head, a forehead groove, drop-shaped eyes with the point on the exterior and a hollowed out circle in the middle, and a slit-shaped mouth with trapezoidal outlining (Menzel, 1967:23–25 and Plates XVI–33 to 35, XVII–36 to 38; *see also* Menzel, 1966:88–89 and Kroeber and Strong, 1924:Plate 14, top row). Like one of the Chincha examples illustrated by Menzel (1967:Plate XVI–34), the piece from Lo Demás has traces of paint (though not in an identical pattern): red on the right side and a dark (black?) triangle on the forehead, with the point of the triangle resting on the nose (paint not shown on Fig. 33).

The Lo Demás head has only two important differences from the Chincha style figurine canon: the ears are not pierced (although they do have indentations), and a white slip does not cover the surface. However, the white slip could have worn off—the piece comes from a midden, it is broken, and the black and red paint are poorly preserved, all of which suggest that the head might have been handled extensively before being discarded. Two incisions marking the nostrils on the Lo Demás figurine head represent a minor variation from the Chincha style canon; according to Menzel (1967:24), "nostrils are not indicated on Chincha figurines." Nostril-marking is a feature of the earlier, Ica 6 unbaked clay figurines (Menzel, 1967:22).

The other two figurine fragments from Sector I were found together in Feature 120 in Subunits 1C and 10D (Fig. 34), a shallow depression filled with midden and a variety of unusual objects: the two figurine fragments, a small, conical wooden object, a cane or maize leaf carefully shredded into strands and woven into a loose net, and six small balls of dense, concreted sand. Both figurine fragments are made of solid clay fired to an orange color with a cream-colored core, and both show traces of white

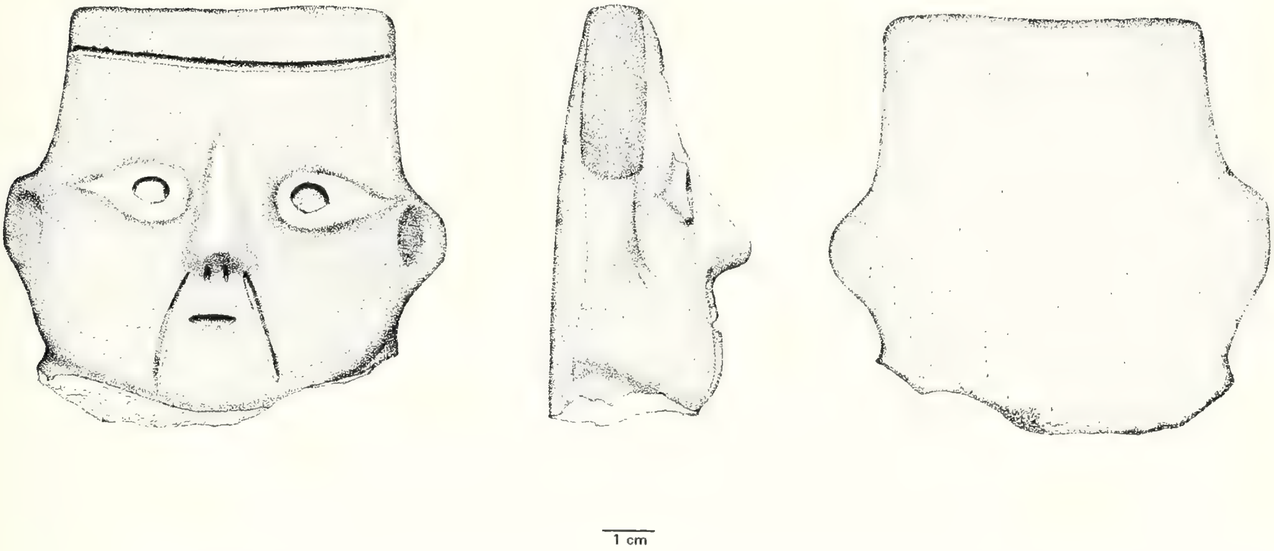

Fig. 33.—Chincha style ceramic figurine from Lo Demás, Sector I, Subunit 3B, level 7c, Stratigraphic Complex C (cat. 1124). Traces of red and black paint on the face are not shown because of the paint's poor preservation, which made it difficult to determine the original form and extent of this decoration.

slip; the two pieces may have come from the same figurine. Unlike the figurine head from Subunit 3B, however, the two pieces from 1C/10D fit Menzel's south coast Late Horizon figurine style (Menzel, 1967:25–30 and Plates XVIII–39 to 42, XIX–46 to 48; *see also* Kroeber and Strong, 1924:Plate 14, lower right) rather than her LIP 8/early LH Chincha figurine style. The grooved forehead, squared head, and white slip on the 1C/10D head fragment (Fig. 34a) are features shared between some examples of the two styles; however, the eye form on this piece is diagnostic of the Late Horizon style. Menzel describes the Late Horizon eyes as

> "lenticular appliqués oriented approximately horizontally, with a lenticular groove separating the area of the pupil from the rest of the eye . . . . This is an eye form used in Inca figurines and may constitute an imitation of Inca eyes in the south coast style" (Menzel, 1967:27).

The sample of south coast LH figurines studied by Menzel also had eyes outlined with paint (Menzel, 1967:27), a feature not present on the Lo Demás specimen.

The leg fragment from Feature 120 supports the LH style attribution of the head (Fig. 34b). The LIP 8 Chincha style figurines have separated legs, while the LH south coast style examples have their legs joined. The leg fragment from Lo Demás had orig-

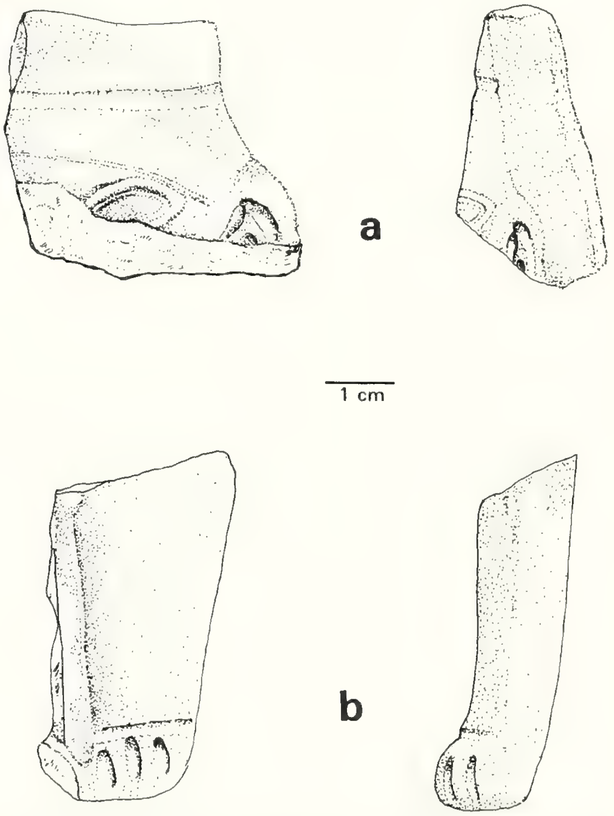

Fig. 34.—South coast Late Horizon style ceramic figurine fragments from Lo Demás, Sector I, Subunits 1C and 10D, feature 120, Stratigraphic Complex C (cat. 848).

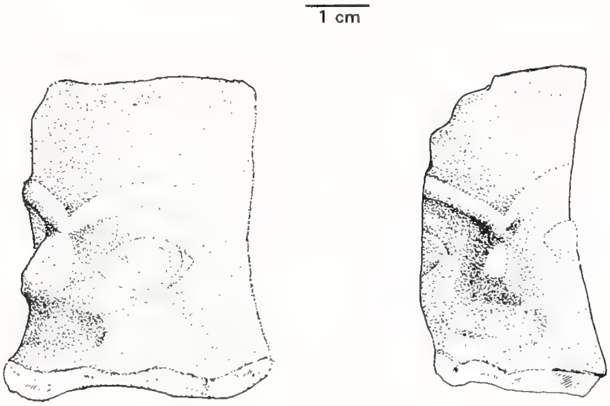

Fig. 35.—Pachacamac-Inka blackware faceneck jar rim sherd from Lo Demás, Sector I, Subunit 4A, level 4, Stratigraphic Complex D (cat. 520).

inally been joined to its pair, as demonstrated by the rough, broken surface on the inside of the leg.

Two pottery finds from the excavations in Sector I have anthropomorphic modelling. One is a blackware sherd from a faceneck jar found in Subunit 4A, Stratigraphic Complex D (Fig. 35). This sherd differs markedly from Menzel's LIP 8/early LH Chincha style faceneck jars in rim form and diameter, and in details of the face (Menzel, 1966:Plate IX–1, 7). Rather, like the Feature 120 head fragment, the eyes of the Lo Demás jar face are the diagnostic grooved, lenticular appliqués of Menzel's (1967) LH south coast style. In her analysis of late Chincha pottery, Menzel (1966:112–113 and Plate XV–65; *see also* Kroeber and Strong, 1924:10, Fig. 1f) discusses and illustrates a blackware, faceneck jar which she identifies as "Pachacamac Inca" and places in her later LH "post-Chincha assemblage." The face on this jar is similar to the Lo Demás specimen except that the specimen illustrated by Menzel and Kroeber and Strong lacks the heavy, modeled eyebrow (or browridge) of the Lo Demás face. Also, the rim on the Menzel/Kroeber-Strong vessel is more everted than the Lo Demás rim. However, Uhle illustrates two blackware faceneck jars from Pachacamac which do have modeled eyebrows identical to the Lo Demás specimen (Uhle, 1903:65, Fig. 79 and Plate 18–2); the rims on the Pachacamac jars are slightly less everted than the Menzel/Kroeber-Strong specimen. Both of the Pachacamac examples came from Late Horizon contexts, the first (Uhle, 1903:Fig. 79) from "graves in the outer city[,] Inca period of the coast land" and the second (Uhle, 1903:Plate 18–2) from the "Cemetery of the Sacrificed Women, Sun Temple."

The second pottery find with anthropomorphic modelling came from Subunit 10D, Stratigraphic Complex B. This find consists of three oxidized, reddish-orange, unpainted sherds with a modeled arm and hand (Fig. 36); two of the sherds fit together and the third, with the hand, clearly belongs to the same vessel. Similar arms and hands are modeled on the side of the "Pachacamac Inca" blackware

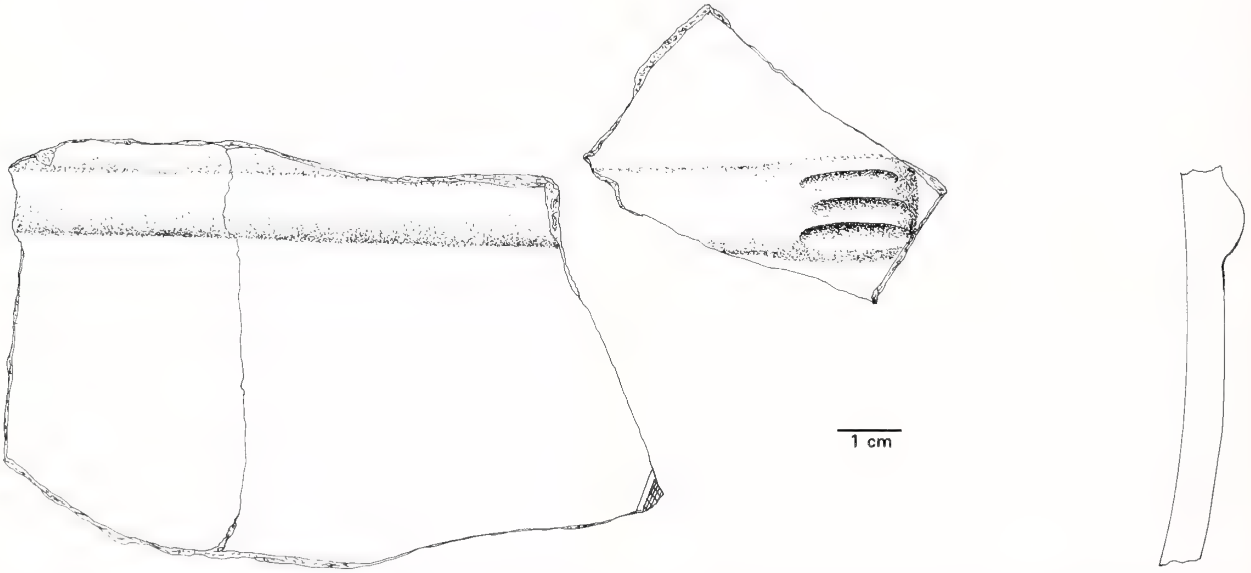

Fig. 36.—Pottery sherds with modelled hand and arm, from Lo Demás, Sector I, Subunit 10D, level 24, Stratigraphic Complex B (cat. 1391).

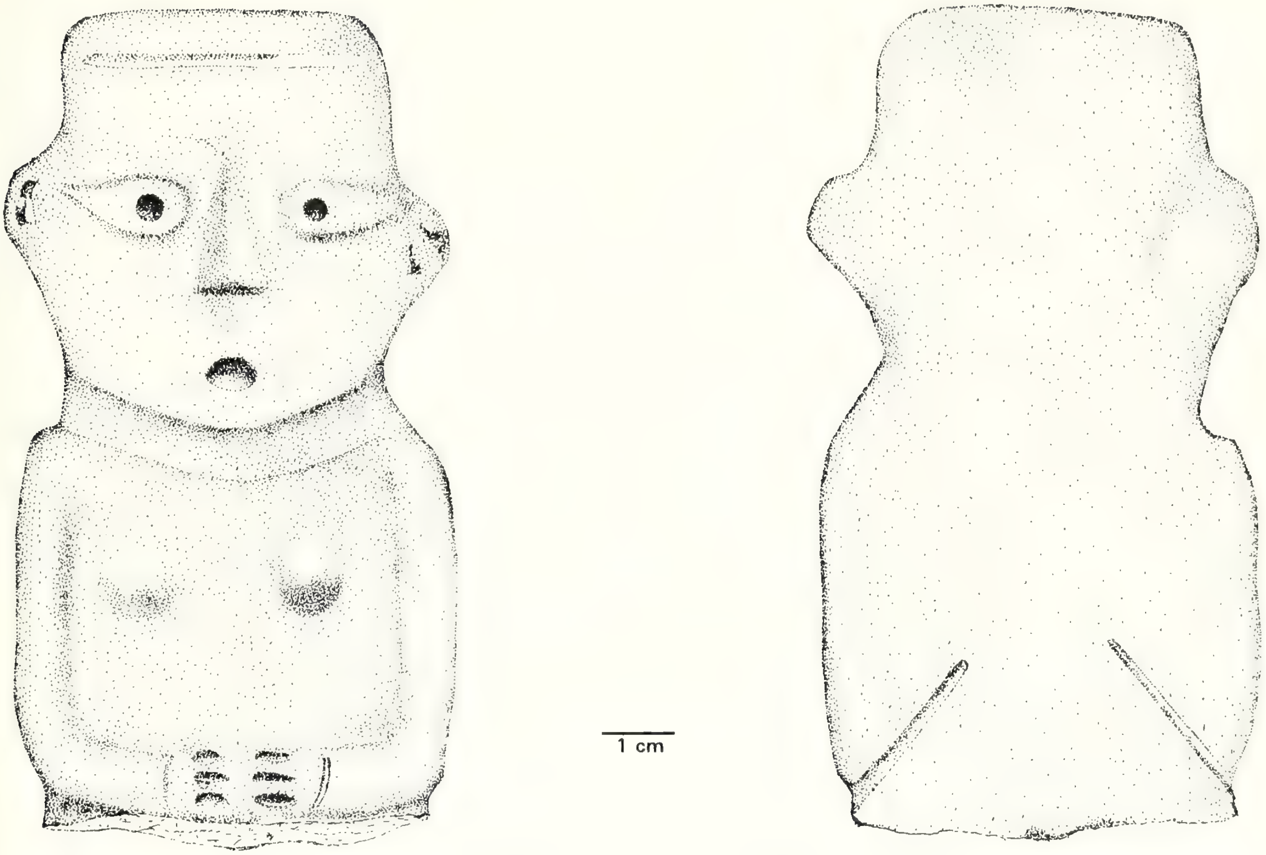

Fig. 37.—Chincha style ceramic figurine from Lo Demás, Sector IV, quebrada profile, from a level equivalent to 12d in Subunit 26D.

faceneck jar illustrated by Menzel (1966:Plate XV–65). Although one of the Chincha style faceneck jars does have short, modeled arms which extend from the shoulder to the neck as tubular handles (Kroeber and Strong, 1924:Plate 12d), no features like the Lo Demás and Pachacamac Inka arms and hands are seen on any of the Chincha style vessels which Menzel illustrates. Therefore, it seems likely that the arm/hand sculpture on the Lo Demás vessel is a Late Horizon feature, an attibution supported by the close proximity of this sherd to the Cuzco Polychrome A sherd (Fig. 29c).

Sector IV Figurines

Two figurine fragments were excavated from Subunit 26D, and one (two-thirds complete) figurine from stratigraphic context in the quebrada profile adjacent to 26D, in a level equivalent to 26–12d. This latter fragment is the head and torso of an adult female figurine, as indicated by the two small mounds representing breasts; only the legs are missing (Fig. 37). The solid, fired, tan-orange clay construction, traces of white slip, square head, forehead groove, tear-drop eyes with circular depressions, and position of the lower arms and hands identify this piece as a Chincha style figurine (Menzel, 1967:23–25). Like the head from Subunit 3B in Sector I (Fig. 33), the quebrada profile figurine's ears are not fully perforated. It has a smaller head than the 3B specimen and the mouth is not set off by trapezoidal markings.

The other two Sector IV figurine fragments are harder to identify. One is a solid, tan-colored, fired clay leg with incised toes, from level 26–14b (Fig. 38a). Because the leg was not joined to its pair, it can tentatively be assigned to the Chincha style. The second fragment, from Feature 2613i, is a hollow, blackware leg or other appendage with three parallel incisions (Fig. 38b). Menzel (1966:98, 1967:24 and Plates XVI–35, XVII–36) describes the infant variant of Chincha style figurines as hollow, but no blackware Chincha style examples are known for any of the variants, nor does the form of the 26D

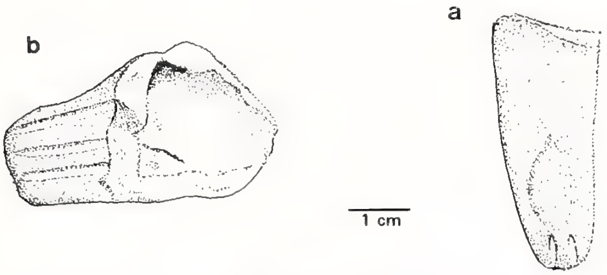

Fig. 38.—Ceramic figurine fragments from Lo Demás Sector IV, Subunit 26D. a) From level 14b (cat. 1853). b) From feature 2613i (cat. 1864).

specimen resemble that of the infant variant figurines' appendages.

Chronological Significance of the Lo Demás Figurines

The presence of both LIP 8/early LH Chincha style and LH south coast style figurines in the same stratigraphic complex (C) in Sector I strongly suggests that the Chincha style remained in use throughout the Inka occupation of Chincha, rather than being replaced shortly after the Inka conquest by the post-Chincha assemblage, as Menzel (1966) claims (analysis of the Lo Demás pottery also suggests this conclusion—*see* Chapter 7). In fact, Menzel (1967:23) writes that "one figurine of [the Chincha] style was found in a later burial of the Inca occupation period, where it represents either the continued use of this style of figurines or possibly an heirloom."

The Chincha style probably does represent the local tradition (Menzel and Rowe, 1966:64) and therefore probably began before the elements of the post-Chincha assemblage were present in Chincha. However, although Menzel (1966:79, 97; 1967:23; Menzel and Rowe, 1966:64–65 and Plate VIII) sees a chronological division of the two styles shortly after the Inka conquest of Chincha, there seems to be no compelling reason to regard the two "units of association" as chronologically distinct during the Late Horizon. The co-occurrence of Inka (or Inka-related) and Chincha style pottery and figurines in the Lo Demás excavations implies the first of Menzel's explanations for the presence of a "Chincha style" figurine in an Inka burial, namely, continued use of the Chincha style throughout the Late Horizon (*see* Chapter 11).

A similar situation apparently occurred at the Cañete valley fishing site of Cerro Azul. Marcus (1987*b*: 37–38, Figs. 21, 22) illustrates a series of seven figurines from burials and structures assigned to the Late Intermediate Period (Marcus, 1987*b*:25). Six of the seven Cañete figurines closely resemble the Chincha style figurines, a resemblance noted elsewhere for the Cañete figurine style in general (*see* Menzel and Rowe, 1966:65; Kroeber, 1937:246–247). The seventh Cerro Azul figurine from Marcus's collection (Marcus, 1987*b*:38, Fig. 22b), however, fits Menzel's (1967:25–29) south coast Late Horizon style, most notably in the lenticular, grooved, painted eyes[67] and in the joined legs (*see* Sandweiss, 1989:284, footnote 162). Presumably, other Late Intermediate Period features on finds from the same context (e.g., the figurine in Marcus, 1987*b*: 38, Fig. 22d) led Marcus to assign an LIP date to this piece; as at Chincha, the co-occurrence of LIP and LH style pieces in the same context argues for the continuation of the local Cañete style throughout the Late Horizon (and greater caution in assigning dates to structures with Late Cañete style contents). The fact that "virtually no Inca pottery has been discovered so far at Cerro Azul, even in those buildings with Inca architectural features" (Marcus, 1987*b*:95) supports the hypothesis that the local pottery styles continued in use throughout the Late Horizon in Cañete as well as Chincha.

METAL OBJECTS

Only a few pieces of metal were recovered from the excavations in Sector I of Lo Demás (Table 9); none were found in the Sector IV excavations. However, part of a collection of metal objects reportedly pulled from the quebrada profile in Sector IV offers further insight into the use of metals in late pre-Hispanic Chincha.

The ethnohistoric record also provides information on Chincha metallurgy (*see* Chapter 2). As Menzel and Rowe (1966:68) point out, "at the time of the Spanish conquest, Chincha had a notable reputation for wealth in precious metals, especially silver." Gold and silver objects were extensively looted from Chincha burials in the early Colonial Period, and Uhle (1924; Kroeber and Strong, 1924) found metal objects—mostly silver—in many of the late Chincha burials which he excavated in 1901.

In addition to the sources for early Chincha looting cited by Menzel and Rowe (1966:68 and footnote 29), the "Aviso" document states that when Hernando Pizarro had the natives of Chincha in *encomienda,* he sent two men to the valley to obtain gold and silver. They met with great success; from an area which probably lay close to El Cumbe and

Table 9.—*Metal objects from Sector I, Lo Demás. Abbreviations: Complex, stratigraphic complex in Sector I; Cat., catalogue number (Sandweiss, 1989:Appendix B).*

Cat.	Sub-unit	Complex	Description
387	2D	D	copper hook: question-mark form, upper shaft square, hook curve cylindrical, hook point flattened; overall length: 22.09 mm; hook diameter: 9.00 mm; thickness: 1.02 mm upper shaft, 1.07 mm hook curve, 0.08 mm flattened hook point; weight: 0.420 g before treatment, 0.270 g after treatment
724	4D	D	small, irregular piece of copper; length: 11.05 mm; maximum width: 8.02 mm; minimum width: 7.00 mm; thickness: 3.04 mm
1475	4B	C	small bit of copper, completely oxidized
1471	3B	B	copper wire fragment with one end pointed; length: 48.01 mm; maximum thickness: 2.03 mm; minimum width: 2.00 mm; possibly part of a "tupu" pin
1742	2C	B	small piece of copper oxide
1772	2B	B	rectangular silver sheet, fragment of a larger piece; length: 22.02 mm; maximum width: 10.00 mm; minimum width: 8.03 mm; thickness: 1.08 mm; covered with greenish oxide

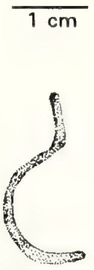

Fig. 39.—Copper fishhook from Lo Demás, Sector I, Subunit 2D, level 3d, Stratigraphic Complex D (cat. 387). See Table 9.

La Centinela (*see* Fig. 1), they recovered "one hundred thousand marks of silver in large and small vessels and other insects and snakes and small dogs and deer all in gold and silver" ("Aviso," Rostworowski, 1970:171–172). The "Aviso" (Rostworowski, 1970:168–169) also mentions occupationally specialized gold- and silversmiths, though the author of this document was referring to the Inka empire in general when he discussed the metal workers (*see* Chapter 2).

Enrique Retamozo (1984*a*, 1984*b*, 1985) carried out the technical analyses of metal remains from Lo Demás. Of those from excavation contexts in Sector I, five are copper and one is silver. Three of the copper pieces are too small and corroded to provide any other information. One copper artifact from Stratigraphic Complex B (Table 9:cat. 1471) is a pointed piece of thick wire which Retamozo (1985) believes to have been part of a *tupu* or cloak pin used to fasten women's mantles (*see* Rowe, 1946: 235, Fig. 79a, b). The "Aviso" (Rostworowski, 1970: 168–169) mentions these pins as an example of the light pieces which the gold- and silversmiths of the Inka empire could make for their own gain (*see* Chapter 2).

The final copper object from Sector I consists of a small, question mark-shaped fishhook from Complex D (Fig. 39, Table 9:cat. 387). The upper shaft is square, the curve of the hook is round, and the point is flattened; according to G. Schworbel (Museo Nacional de Antropología y Arqueología, Lima), these attributes are characteristic of late pre-Hispanic Peruvian fishhooks (personal communication, 1984). The Lo Demás hook is evidence of fishing by the late pre-Hispanic inhabitants of the site. The majority of fish remains recovered from Lo Demás come from small species (*anchovetas* and sardines), most of which were probably captured by netting (*see* Chapter 9). However, among the fish remains are elements representing a small number of medium-sized fish of the order Perciformes (*see* Chapter 9), which range from 20 to 60 cm in average length at maturity (Mariano A., 1984; Sánchez, 1973). The Lo Demás hook is appropriate in size for these fish.

The excavated remains from Sector I include one silver object, a piece of sheet silver broken from a larger object whose original form and function cannot be determined (Stratigraphic Complex B; Table 9:cat. 1772). A greenish oxide covers the surface of this piece, suggesting that it may be made of a silver/copper alloy.

The collection of copper pieces loaned to me by Sr. Jesús Pachas, of Sunampe and Tambo de Mora, is of particular interest because it appears to come from a metallurgical workshop (Retamozo, 1984*a*). According to Sr. Pachas, the collection (which now consists of 53 pieces weighing a total of 2,024.3 g, *see* Sandweiss, 1989:Appendix C) represents about one fourth of the metal pieces originally found several years ago in a cloth bag eroding from the que-

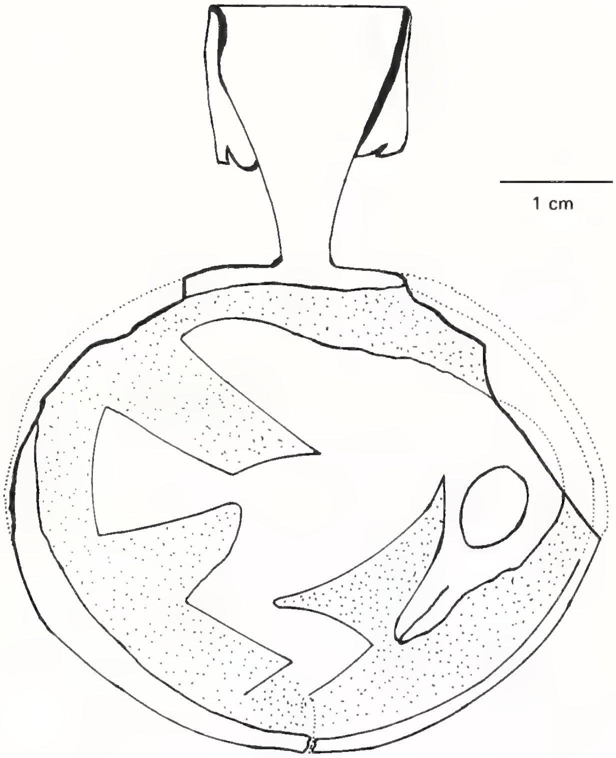

Fig. 40.—Copper tweezers, Pachas collection from Lo Demás, Sector IV (Sandweiss, 1989:Appendix C: #1).

brada profile in Sector IV of Lo Demás, just north of Building IV–2 and about a meter below the surface.

The decoration on one piece, a "pinza" or tweezers, confirms the late pre-Hispanic date of the metal collection (Fig. 40) (Sandweiss, 1989:Appendix C–1). The shape of the tweezers corresponds to Kroeber and Strong's (1924:39–42) Type 7, in their typology of tweezers from Uhle's Chincha gravelots. Kroeber and Strong found Type 7 tweezers in graves of their Late Chincha II period and in graves with mixed or doubtful associations. Late Chincha II corresponds to Menzel's (1966) post-Chincha assemblage, which she considers to be the part of the Late Horizon during which the Inka controlled Chincha (*see* Chapters 4, 7, and 11).

The bird design on the tweezers is incised, with the background stippled in contrast to the smooth body of the bird (Fig. 40). The bird is long-necked, with a single, large round eye, long legs, a triangular tail, a swept-back wing, and a body of indeterminate form. In part, the form of the design is constrained by the shape of the decorated surface; nevertheless, the tweezers bird closely resembles the birds painted on the walls of Room IV–1a in Building IV–1 in Sector IV of Lo Demás, especially in the form of the eye, wing, and tail (compare Fig. 40 with Figs. 16 and 17). It is even more similar to the birds on three round, incised metal ear plugs from graves excavated by Uhle (Kroeber and Strong, 1924:43, Fig. 25a–c). In the case of one plug (Kroeber and Strong, 1924:Fig. 25b), the resemblance verges on identity, the only difference being that the ear plug shows two mirror-image birds connected at the feet. Furthermore, "in all three specimens [from the Uhle collections] the disk pattern consists of smooth bird figures surrounded by embossing or stippling" (Kroeber and Strong, 1924:43). Kroeber and Strong found the bird-decorated ear plugs only in graves which they classify as Inka and Late Chincha II (Late Horizon), confirming the late date of the metal collection and its contemporaneity with the excavated deposits in Sectors I and IV of Lo Demás.[68]

The bird tweezers are the only piece in the metal collection that bears a decoration and is part of a finished artifact; the rest of the material consists of pieces of metal broken while being worked (Sandweiss, 1989:Appendix C–Group I), bits of metal laminae cut off from larger sheets (Sandweiss, 1989: Appendix C–Group II), and pieces of metal that had been poorly founded (Sandweiss, 1989:Appendix C–Group III) (Retamozo, 1984*a*). Even the tweezers may have been broken during the final stages of preparation. The collection resembles the kind of debris generated by metalworking,[69] indicating that it originally came from a metallurgical workshop.

The Sector IV metal collection raises a series of questions. Where was the workshop which produced the pieces? If it was not at Lo Demás, why was the collection found there? What does the collection indicate about specialization? The fishing site has no traces of copper slag or of large ash deposits, much less of smelting furnaces such as those Shimada et al. (1982) describe for the north coast; thus, the workshop was not part of Lo Demás (at least not the surviving portion of the site). The Chincha style decoration on the bird tweezer suggests that the workshop was in Chincha. A surface collection made in 1984 along the bluff to the north of Lo Demás contains a number of metal ojects, including a metalworking tool called a "cincél" or chisel (Vivanco, 1987:99). This object was found ca. 5 km to the north of Lo Demás and had apparently eroded from a grave on top of the bluff. The same site yielded 23 pieces of metal very similar to the Pachas collection: sheet fragments and poorly founded or broken pieces of copper (Vivanco, 1987:97, Cuadro 4).

Sixteen more laminae came from a nearby site, a few hundred meters along the bluff. The cincél site (Vivanco, 1987:99–100) also produced a complete copper bowl in a typical south coast form, the shallow dish with basal flange (Menzel, 1976:39–42 and Plates 3–48 to 57, 19–225 to 227).[70] Other finished metal artifacts of various types were found at a number of other locations along the bluff (Vivanco, 1987: 93–102). All of these surface finds (from disturbed burials) suggest that a metallurgical workshop was located somewhere near the bluff to the north of Lo Demás and might be found by further field work.

Given that the workshop was not part of Lo Demás per se, why was a collection of workshop debris located in Sector IV? One explanation is that, although located elsewhere, the metalworkers were specialists attached to the fishing lord who presumably resided in Sector IV of Lo Demás,[71] a relationship similar to that enjoyed by gourdworkers (*see* section on gourds below and Chapter 10).

An alternative hypothesis is that the bag of metal debris represents either trade goods or the pieces of copper which the "Aviso" (Rostworowski, 1970: 171) says were used by the merchants to buy and sell food and clothing. Rostworowski (1970:154) believes that the merchants of Chincha obtained metal from the southern highlands[72] and sent it north by sea to Ecuador to trade for *Spondylus* shell and other items. The collection of copper pieces could have been intended for trade in the north; the fishermen would certainly have been involved in the maritime trade, at the very least as crew for the trading rafts.

There is a discrepancy between the Lo Demás and related finds on the one hand and the documents and Uhle's discoveries on the other. The early sources mention gold and silver and their respective smiths, and Uhle found mostly silver in the Chincha burials, but the materials found in Lo Demás consist almost entirely of copper. According to the "Aviso" (Rostworowski, 1970:168–169), the gold- and silversmiths did not pay tribute, but instead made objects for the Inka and at his behest for other lords. However, the "Aviso" does not mention copperworkers, though it does say that copper was a medium of exchange in the valley. The documentary evidence thus suggests that if there were metalworkers attached to the fishing lord, they were dependent specialist coppersmiths, not independent specialist gold- or silversmiths. The "Aviso" (Rostworowski, 1970: 171) states that in Chincha, copper had a fixed rate of exchange for gold and silver. This, in turn, suggests an articulation between two different circulation networks, one for copper and one for precious metals. The predominance of copper in the limited collection of metal recovered from Lo Demás supports this interpretation of the documents. In this context, the archaeological evidence suggests that metallurgical workshops were specialized in copper or in precious metals, and that different metals circulated through different routes within Chincha society.

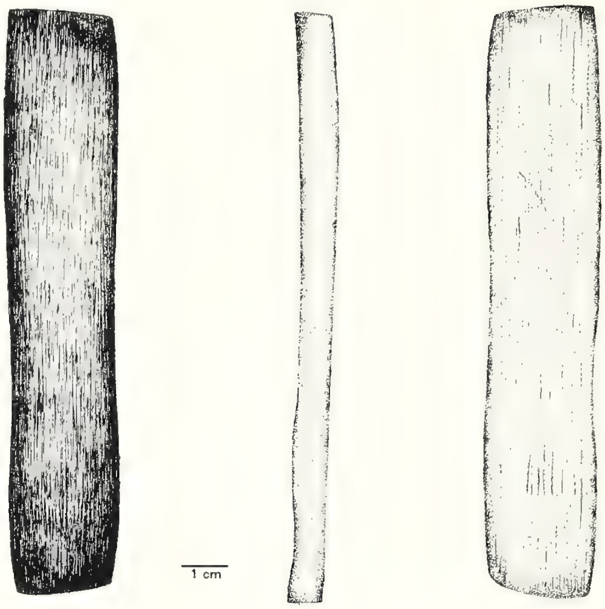

Fig. 41.—Wooden *mallero* (net-making tool) from Lo Demás, Sector I, Subunit A2, level 3bii, Stratigraphic Complex C (cat. 52).

Wooden Objects

We found three classes of wooden artifacts during the excavation of Sector I, two represented by one specimen each and one represented by 17 specimens. One of the unique objects is a net-making tool; the second is probably a weaving tool. The function of the third class is uncertain. The deposits in Sectors I and IV also contained pieces of wood which appear to be debris from woodworking.

Mallero (Net-gauge)

A *mallero* is a tool used to make and repair nets. *Malleros* are rectangular, with squared ends; the dimensions of the tool dictate the mesh size of the net to be made. Different mesh sizes are used for different classes of fish. The *mallero* from Lo Demás (Fig. 41) came from Stratigraphic Complex C in Subunit A2. It is made of a hard, dark wood and

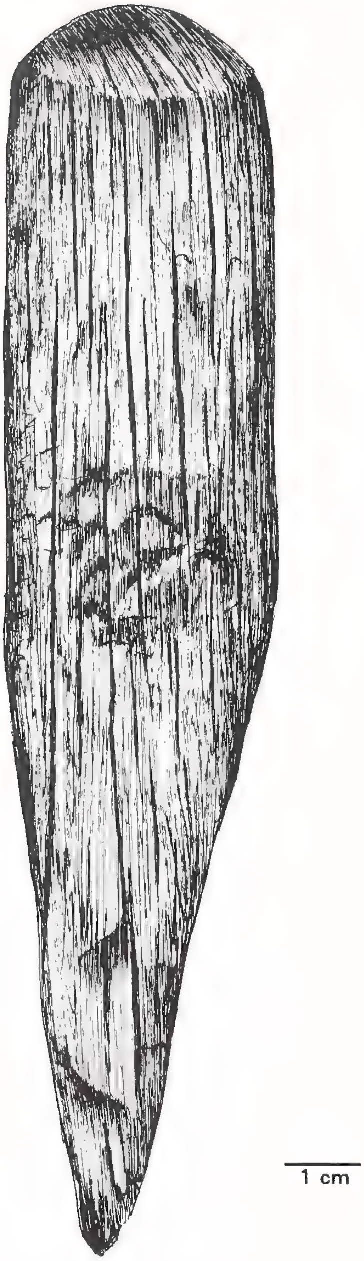

Fig. 42.—Wooden *ruqqui* (weaving tool) from Lo Demás, Sector I, Subunit IA, feature 117W, Stratigraphic Complex C (cat. 749).

has a surface polish that probably reflects use. The *mallero* is 12.75 cm long and 2.39 cm wide, with a maximum thickness of 1.00 cm along the longitudinal centerline and less on the edges. According to traditional fishermen in Tambo de Mora, the Lo Demás *mallero* is appropriate for small-mesh nets of the kind used to catch small schooling fish such as *anchovetas* and sardines, the two predominant fish species in the Lo Demás midden (*see* Chapter 9).

The use of *malleros* in pre-Hispanic Peru is well known. One example close in time, space, and context was found by Marcus (1987*b*:73, Fig. 47B) in the Late Intermediate Period component of the Cerro Azul fishing site in Cañete, the next valley to the north of Chincha; this specimen is also made of wood and measures approximately 8.5 cm by 2.3 cm (thickness could not be determined from the published illustration). A possible bone mallero found in Sector IV of Lo Demás (*see below,* section on Bone and Shell Objects) indicates that a variety of materials may have been used to make this class of tool.

Ruqqui

A wooden object (length = 16.08 cm, diameter = 3.78 cm) resembling a stake was recovered from Stratigraphic Complex C in Subunit 1A of Sector I (Fig. 42). This specimen is cylindrical, with one end bilaterally planed to form a blade. The other end is slightly rounded. Bernardino Ojeda (Centro de Investigaciones de Zonas Aridas, Lima) identified the Lo Demás stake as a "ruqqui," a tool used in weaving to tighten the textile on the loom. Gonçalez Holguin (1952 [1605]) defines *ruqqui* as "the bone with which they tighten" textiles ("el huesso con que tupen"). A similar tool made of bone was found in Subunit 26D in Sector IV (*see below,* section on Bone and Shell Objects).

A number of wooden implements were recovered from Chincha graves by Uhle (Kroeber and Strong, 1924:34–35 and Fig. 16). "Wooden pegs or stakes" range in length from 25 to 50 cm (significantly longer than the Lo Demás specimen) and have a consistent diameter (unlike the Lo Demás stake). The Uhle collection also has three types of wooden objects with flattened ends (Kroeber and Strong, 1924:35 and Fig. 16). The Lo Demás stake most closely resembles the first of these types (Kroeber and Strong, 1924:Fig. 16g–k),[73] but it is significantly shorter and lacks a knob. Kroeber and Strong do not assign a function to this type of wooden object, though they suggest that larger wooden tools with flattened ends from the Uhle collection were used in agricultural work (*see also* Kvietok, 1987, for a discussion of south coast digging sticks). Given the differences between the Lo Demás stake and the wooden implements described by Kroeber and Strong (1924),

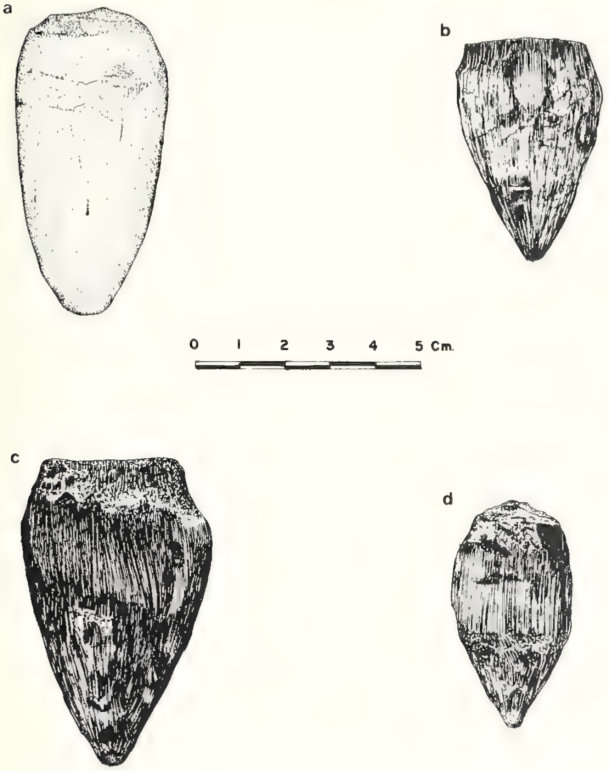

Fig. 43.—Conical wooden objects from Lo Demás, Sector I, Stratigraphic Complex C. a) and b) From Subunit 2B, level 8b (cat. 834). c) and d) from Subunit 3A, level 5di (cat 856). See Table 10.

Table 10.—*Conical wooden objects. Abbreviations: Complex, stratigraphic complex in Sector I; Cat., catalogue number (Sandweiss, 1989:Appendix B); Diameter, maximum diameter; H/D, ratio of height to maximum diameter. All measurements are in cm.*

Cat.	Subunit	Complex	Level	Height	Diameter	H/D
		Sector I				
17	A1	D		5.2	2.4	2.2
19	A2	D		6.3	irregular shape	
19	A2	D		3.5	2.0	1.8
294	2B	D		5.7	2.2	2.6
425	2D	D		5.4	2.8	1.9
834	2B	C		6.6	3.4	1.9
834	2B	C		3.7	3.2	1.2
834	2B	C		6.7	4.4	1.5
856	3A	C		6.8	4.1	1.7
856	3A	C		4.9	2.7	1.8
917	2B	C		4.6	2.6	1.8
917	2B	C		5.1	3.0	1.6
917	2B	C		5.0	3.1	1.6
1907	Col. I	C		5.7	3.0	1.9
1750	2C	B		6.5	2.7	2.4
		Sector IV				
Cat.	Subunit		Level	Height	Diameter	H/D
1725	26D		26-4c	4.0	4.0	1.0
1851	26D		26.13b	4.0	2.4	1.7

the use of the stake as a farming tool seems unlikely and its identification as a weaving *ruqqui* is the best interpretation.

Conical Objects

The 17 conical wooden objects from Lo Demás vary in exact dimensions but share a general design (Fig. 43, Table 10). All have a cylindrical body with one end narrowed to a point and the other end cut off flat; the circumference of the object on the flat end is often reduced, resulting in a sort of "waist" (Fig. 43b–d).

These objects were recovered from the three major stratigraphic complexes (B to D) in Sector I and from Subunit 26D in Sector IV. Most came from Complex C in Sector I, where the majority of the specimens were found in groups of two (Table 10: cat. 856) and three (Table 10:cat. 834, 917). These groups occurred in a horizontally and vertically restricted area and probably were all deposited together.

The function of the conical wooden objects from Lo Demás is difficult to determine. The items belong to a class of common coastal artifacts usually referred to in Peru as "flotadores" (floats) because of their superficial resemblance to net floats. However, there is no direct evidence to support this functional attribution; to my knowledge, no conical wooden "flotador" has ever been found attached to a net, though gourd floats have been found tied to nets in Andean coastal sites dating as early as the Late Preceramic Period (Bird et al., 1985:225, Fig. 171). On the other hand, many of the specimens from Lo Demás were covered with salt crystals, which may be evidence for immersion in salt water, albeit weak, because the salt air of the coast can permeate the archaeological deposits.

An alternative explanation is bottle stoppers. Rogger Ravines (personal communication, 1984) recalled seeing similar objects used as bottle stoppers in the Peruvian highlands, and he suggests that they may have had the same function in pre-Hispanic coastal sites. The bottle stopper hypothesis would account for the variation in size of the different specimens (in accordance with variable bottle mouth sizes); bottles are a fairly common form in the Lo Demás pottery assemblage (Fig. 25). The

Table 11.—*Wood fragments. Abbreviations: Su, Subunit; SC, stratigraphic complex in Sector I; Cat., catalogue number (Sandweiss, 1989:Appendix B). Codes: Fi, fibrous; Fr, fragment; Fr+R, fragment with rounded end; HE, outer rings of tree; L, lustrous; PC, partially cut; Po, porous; S, smooth; WC, wood chip; +B, with bark; +C, charred. Measurements are in cm. Widths are maximum/minimum.*

Cat.	Su	SC	Level	Texture	Type	No. Cuts	Length	Width
Sector I								
365	3A	D		Po+C	F	0	9.1	1.3/0.5
404	1B	C		S	PC	2		
404	B	C		S	PC	1		
498	1C	C		S	HE	0		
1242	3B	B		S	PC	1	5.3	1.2/0.2
1590	2B	C		S+C	F	0		
1591	2B	C		S	PC	?		
1669	2A	B		Fi	WC	2	2.5	2.5/0.6
1701	2A	B		Fi	Fr	0		
1701	2A	B		Fi+C	Fr	0		
1729	2C	B		S	HE	0		
1729	2C	B		Fi	WC	2		
1730	2C	B		Fi	WC	2		
1730	2C	B		S+B	PC	1		
1732	2C	B		Po	Fr	0	0.9	
1732	2C	B		Po	Fr	0		
1732	2C	B		Po	Fr	0		
1733	2C	B		S+B	Fr	0		
1750	2C	B		Fi	WC	2		
1774	4D	B		S	HE	0		
1774	4D	B		S	Fr	0		
1774	4D	B		Po	Fr	0		1.0
1827	4B	B		S	PC	10	10.0	3.3/0.4
1833	4B	B		S	PC-HE	2	8.3	4.0/0.3
1833	4B	B		P	Fr	0		
Sector IV								
1681	26D		2	Po	Fr	0		
1681	26D		2	Po	Fr	0		
1725	26D		4c	S+C	Fr	0		
1725	26D		4c	S+C	Fr	0		
1726	26D		5	S+C	Fr	0		
1726	26D		5	Po	Fr	0		
1726	26D		5	Po	Fr	0		
1726	26D		5	Po	Fr	0		
1726	26D		5	Po	Fr	0		
1726	26D		5	Fi	WC	2		
1726	26D		5	S	PC	1		
1727	26D		5i	Fi	WC	1		
1727	26D		5i	Fi	WC	1		
1727	26D		5i	Fi	WC	1		
1727	26D		5i	Po	Fr	0		
1788	26D		f.2603i	S	PC	1		
1810	26D		12i	Fi+C	Fr	0	0.7	0.9/0.2
1823	26D		17i	S+B	Fr	0	3.3	5.1/0.9
1838	26D		12c	Po	Fr	0		
1838	26D		12c	Po	Fr	0		
1838	26D		12c	Po	Fr	0		
1838	26D		12c	Po	Fr	0		
1838	26D		12c	Po	Fr	0		
1838	26D		12c	S	HE	0	1.1	0.1
1838	26D		12c	S	PC	3	5.0	1.1/0.4
1839	26D		12d	Po	Fr	0		
1839	26D		12d	Po	Fr	0		
1839	26D		12d	S	PC	2		
1839	26D		12d	S	PC	2	2.0	0.3
1839	26D		12d	S	PC	3	2.0	0.5/0.3

Table 11.—*Continued.*

Cat.	Su	SC	Level	Texture	Type	No. Cuts	Length	Width
1839	26D		12d	S	PC	1		
1839	26D		12d	Fi	WC	2		
1839	26D		12d	S+C	Fr	0	4.0	
1841	26D		13	S	PC	3	5.1	0.2
1841	26D		13	Fi	Fr	0	4.5	
1841	26D		13	Fi	WC	2		0.5
1851	26D		13b	S+C	Fr	0	2.0	1.1/0.3
1851	26D		13b	Fi	WC	2	7.5	0.2
1851	26D		13b	Fi	WC	2		
1851	26D		13b	Fi	WC	2		
1851	26D		13b	Fi	PC	1	3.0	4.0/0.2
1851	26D		13b	S	HE+PC	2	2.2	2.0/0.2
1854	26D		15	S	Fr	0	8.0	3.0/0.3
1854	26D		15	S	PC	2	6.1	0.5/0.3
1854	26D		15	Fi	Fr	0	0.7	1.0/0.7
1854	26D		15	S	PC	1		
1858	26D		16	Fi	Fr	1	1.5	0.7
1858	26D		16	S	Fr	0		0.9
1858	26D		16	Fi	PC	1		
1858	26D		16	Fi	PC	2		
1858	26D		16	Fi	PC	2	1.0	1.5
1861	26D		f.2612	Fi	Fr+R	2	1.2	1.0
1861	26D		f.2612	Fi	PC	2		
	Totals							
Sector I		25						
Complex D		1						
Complex C		5						
Complex B		19						
Sector IV								
Subunit 26D		53						
Combined		78						

average maximum diameter of the conical wooden objects is 3 cm, while the average minimum orifice diameter of the Lo Demás bottle *sherds* is 4 cm; however, the actual average minimum orifice diameter of the *bottles* was probably closer to the maximum diameter of the wooden cones.[74] The conical wooden objects could also be stoppers for gourd bottles (J. Quilter, personal communication, 1991). However, the bottle stopper hypothesis does not necessarily explain why *groups* of the objects were needed. Furthermore, the inflexibility of the wood combined with the rough working of most specimens suggests that the conical wooden objects would not have made very effective stoppers.

As another alternative, Francisco Iriarte (personal communication, 1984) has proposed that these objects were children's tops.

Modified Wood Fragments

This category includes pieces of wood that do not appear to have been artifacts but which show modification (e.g., cut marks), or whose shape suggests that they had been cut from a larger piece. A total of 78 such wood fragments were recovered from Lo Demás, 25 in Sector I (all subunits combined) and 53 in Subunit 26D of Sector IV (*see* Table 11). The majority from Sector I came from Stratigraphic Complex B.

The presence of modified wood fragments implies a limited amount of woodworking at Lo Demás, especially in Sector IV in or around Building IV–2. The frequent presence of cut marks and the fact that few specimens are charred argues against fuel as the primary use of the wood. Kvietok's (1988) analysis of edge damage on selected cobble cortex flakes from Lo Demás indicates that at least one of these flakes was used to work a hard material such as wood (*see below,* section on lithics). Although few cobble cortex flakes were recovered from the same proveniences as wood fragments,[75] such flakes were present in all stratigraphic complexes in Sector I as well as in many levels from Subunit 26D in Sector IV (*see* Table 22). Also present at Lo Demás were pieces of false coral (calcareous heads of polychaete worms);

Table 12.—*Gourd rind fragments from Subunit 10D, Sector I, Lo Demás. Abbreviations: SC, stratigraphic complex in Sector I; Cat., catalogue number (Sandweiss, 1989:Appendix B); P/S, peduncle with stem; G/P, rind with peduncle attached.*

Cat.	SC	P/S	G/P	Body	Rim	Total	Remarks
592	D	0	0	1	0	1	charred on one side
593	D	0	0	2	0	2	
693	C	0	0	2	0	2	
719	C	0	0	0	2	2	
730	C	0	0	1	0	1	possible decoration
791	C	0	0	5	0	5	3 charred
792	C	0	0	5	0	5	1 charred
830	C	0	0	1	0	1	cut
932	C	0	0	1	1	2	rim charred
1089	B	0	0	1	0	1	
1325	B	0	0	1	0	1	bit of pyroengraved design
1326	B	0	0	0	1	1	possible design on exterior; ca. 26 cm diameter
1327	B	0	0	1	1	2	rim ca. 10 cm diameter
1328	B	0	0	1	0	1	possible decoration
1390	B	0	0	4	0	4	1 w/drilled hole and cut sides; 1 with line; 1 possible top of gourd
1391	B	0	0	10	0	10	1 round w/drilled indentation; 1 charred on one end
1418	B	0	0	2	0	2	
1424	B	2	1	13	0	16	1 w/darkened zone
Total		2	1	51	5	59	

Topic (1982:164) found this material in woodworking shops at Chan Chan, where it was used as a rasp for planing and smoothing. These data suggest that woodworking at Lo Demás may have included manufacture of some or all of the wooden artifacts discussed above.

Worked Gourd

Gourd (*Lagenaria siceraria*) rind fragments were common at Lo Demás, as were gourd seeds and, less so, peduncles (*see* Chapter 10).

The gourd samples, from Subunit 10D in Sector I (Table 12) and Subunit 26D in Sector IV (Table 13) differ significantly. Gourd rind fragments, peduncles, and seeds are more abundant in the latter sector, and the percentage of peduncles among all rind fragments in 26D is double that in 10D. Seeds and peduncles are removed in the process of making gourd utensils, implying gourd utensil manufacture in Sector IV of Lo Demás, a hypothesis expanded in detail in Chapter 10.

Gourds apparently were important as containers at Lo Demás. Rim sherds occur in the samples from both sectors, and two of the burials in Sector II had associated offerings of gourd vessels containing food. Uhle also found gourd containers in late pre-Hispanic burials in Chincha associated with pottery belonging to Kroeber and Strong's (1924:36–37) Late Chincha I and Inka "culture styles" (i.e., Menzel's [1966] Chincha style and post-Chincha assemblage, respectively). These vessels apparently all contained cotton and yarn, so the discovery of gourds with food in Sector II of Lo Demás is an important addition to our information on Chincha gourd use.

A number of the gourd rind fragments from Lo Demás had traces of pyroengraved designs, but only two examples are sufficiently well preserved to allow reproduction of the design (Fig. 44). Both specimens are rim sherds and come from Subunit 4B in Sector I (not part of the 10D and 26D samples discussed above), one from Stratigraphic Complex B and one from Complex C. The specimen from Complex C (Fig. 44a) has a row of semi-abstract birds positioned just below the rim; two horizontal lines separate the birds from a geometric design of nested rectangles. The birds resemble those on the ear plug from an early Colonial Period burial (Kroeber and Strong, 1924:43, Fig. 25c) and are even more similar to a Late Horizon Ica 9 (Inka occupation period) design (Menzel, 1976:Plates 34-445 and 56-64a, b).

The second pyroengraved gourd fragment (Fig. 44b) has a geometric design consisting of vertical diamonds with scalloped edges and an interior cross connecting the four points of the diamond. An apparently undecorated zone runs along the rim; the diamonds are separated from this zone by a horizontal line. The total design field seems to be one diamond in width, with a second horizontal line

Table 13.—*Gourd rind fragments from Subunit 26D, Sector IV, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989: Appendix B); P/S, peduncle with stem; G/P, rind with peduncle attached.*

Cat.	Level	P/S	Stem	G/P	Body	Rim	Total	Remarks
1679	1	0	0	0	1	1	2	body w/pyroengraved design; rim is cut
1680	1b	2	2	0	3	0	7	1 body charred
1681	2	0	0	0	8	0	8	1 body charred
1717	3	0	0	0	6	0	61	body w/possible design (scratches)
1718	3b	0	0	0	10	0	10	
1719	4	1	0	1	15	0	16	1 body w/cut mark
1720	4b	0	0	0	8	0	8	
1725	4c	1	0	0	1	0	2	
1726	5	1	0	0	9	0	10	
1738	5bi	0	0	0	0	1	1	cut rim, ca. 27 cm rim diameter
1743	5c	0	0	0	3	0	32	charred, 1 w/cut marks
1744	6	0	0	0	1	0	1	
1765	7b	0	0	0	5	0	5	1 w/cut mark
1777	8	2	0	0	3	0	5	1 body w/cut mark, 1 body w/trace of pyroengraved line
1778	9	2	0	0	8	1	11	1 cut body
1788	f.2603i	0	0	0	1	0	1	
1790	f.2605	0	0	1	2	1	4	rim and 1 body possibly pyroengraved, 1 body charred
1800	10	0	0	2	10	0	12	
1806	11	0	0	0	2	1	3	
1809	12	0	0	1	4	0	5	1 circular cut body w/hole in middle, 1 body is a neck sherd
1811	f.2606	0	0	0	4	0	4	
1839	12d	0	0	0	6	0	6	1 w/incised line, 1 from shoulder w/drilled hole
1841	13	0	0	0	3	0	3	1 w/cut mark
1852	13bi	2	0	0	17	0	19	1 body w/incised line and darkened zone, 1 body w/cut mark
1859	13b	9	0	0	42	0	51	top of one stem slightly charred, 2 bodies w/cut marks
1887	14	1	0	0	5	0	6	1 body cut into round shape
1888	f.2610	0	0	0	8	0	8	2 w/cut marks, 1 cut round w/charred hole in middle
1853	14b	0	0	0	11	0	11	1 round body
1854	15	4	0	0	11	1	16	1 body w/possible pyroengraved design
1858	16	0	0	0	3	0	3	1 possible cut mark
1862	f.2612i	0	0	1	0	0	1	
1863	f.2613	0	0	0	2	0	2	1 cut
1864	f.2613i	1	0	1	2	0	4	1 body w/charcoal on interior, 1 body with cut mark
Total		26	2	7	214	6	255	17 cut, 6 w/design or possible design

running along the base of the field; half-diamonds abut both the upper and lower horizontal lines and alternate with whole diamonds which run from line to line. None of the decorated Chincha artifacts illustrated by Kroeber and Strong (1924) have this pattern, but similar vertical diamonds with interior crosses appear on an Ica 9 (Late Horizon) pot—a vessel which also bears the bird design found on the Complex C pyroengraved gourd (Menzel, 1976:Plate 56–64a, b).

NETS

Net fragments were encountered throughout the excavated deposits in Sector I of Lo Demás. Five large net fragments occurred in situ in the quebrada profile below the 1983 test pits. However, net fragments did not occur in Subunit 26D in Sector IV, nor were any visible in the Sector IV quebrada profile. Fattorini (1984) studied the net fragments from all subunits of the 1983 excavations and DiAnderas (personal communication, 1985) studied those from all subunits of the 1984 excavations.

Analysis of the 1984 collection provides the most detailed information on nets from Lo Demás. The 67 net fragments in this collection came from all three major stratigraphic complexes (B to D), with most concentrated in Complex B (Table 14). In all but one case, the knots are the "simple knot" (d'Harcourt, 1962:105–106 and Fig. 74; *see also* "nudo simple" in Bonavia, 1982:124, Dibujo 42) (Fig. 45A), about which d'Harcourt writes

> "The common netting knot used in Peru is an unstable one. It is a simple (overhand) knot joining the yarn that forms the new mesh row to the center of the corresponding mesh of the

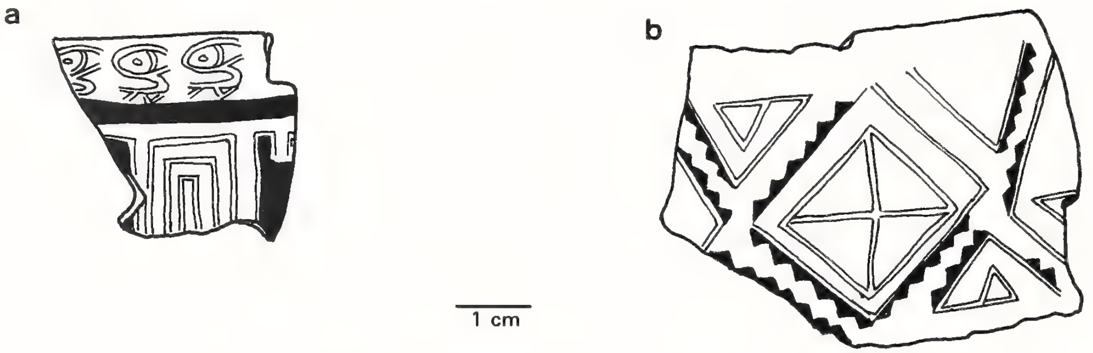

Fig. 44.—Pyroengraved gourd fragments from Lo Demás, Sector I. a) From Subunit 4B, feature 483c, Stratigraphic Complex C (cat. 1713). b) From Subunit 4B, level 24, Stratigraphic Complex B (cat. 1846).

> preceding row. . . . It is in this way that fish nets, carrying nets, and the more delicate nets that are suspended like little bags from the beam bars of scales . . . are made. . . . This knot does not prevent slipping of the cord or yarn it entwines, and this defect can cause a distortion of the network" (d'Harcourt, 1962:105).

One 1984 specimen has a different knot; in Complex B, a net fragment had two varieties of square knot (Fig. 45C and C1) (*see* d'Harcourt, 1962:106–110 and Fig. 76).

All of the net fragments from Lo Demás are made of two-ply yarns. All but four of the 1984 examples are of vegetal fiber (not cotton) and are Z-spun and S-plied (Table 14). Two of the four exceptions, from Complex B, are made of cotton and are S-spun and Z-plied. The other two exceptions, also of cotton, are Z-spun and S-plied, like the vegetal fiber nets.

Complete meshes were preserved on only six of the 1984 specimens, and two of these examples came from the same net. One measure of mesh size, the sum of four sides, ranges from 40 mm to 65 mm (Table 14). This measurement can be translated into three other measures commonly used in Peru: *cuadrado, estirado* or *plana*, and *dedo* (Coker, 1908–II: 57–58). *Cuadrado* refers to the length of one side of the mesh; *estirado* (or *plana*) is measured by pulling the mesh from opposite corners and measuring the maximum extension (= twice the length of an average side, or *cuadrado*); *dedo* refers to the number of fingers that can be placed in one mesh. Though least accurate, the last measure is the one most commonly used by Peruvian fishermen. The sum-of-four-sides is used here as the most accurate and practical measurement on archaeological specimens (Sandweiss, 1989:322, footnote 182).

Coker (1908–II:58) presents a table of *dedo-plana-cuadrado* equivalents for the nets used for different species of fish at the time of his study. That table is reproduced here (Table 15) with the addition of the "sum-of-four-sides" measure (calculated by multiplying Coker's *cuadrado* by four). These data clearly indicate that the mesh sizes of nets from the 1984 excavations in Sector I of Lo Demás are equivalent to those of *pejerreyera* and *anchovetera* nets. The pejerrey (*Odontesthes regia regia*) is a small fish (14–30 cm long, Sánchez Romero, 1973:184), about the same size or a bit smaller than sardines (*Sardinops sagax sagax*) (22–37 cm long, Sánchez Romero, 1973:188) but slightly larger than the *anchoveta* (*Engraulis ringens*) (12–18 cm long, Sánchez Romero, 1973:159). The fish remains in Sector I of Lo Demás consist mainly of sardines and *anchovetas*; pejerrey were not present (Chapter 9). Nets appropriate for pejerreys would be appropriate for sardines, so the net sizes identified for the 1984 collection are entirely appropriate for the fish species found in the same contexts. William Atuncar, a local traditional fisherman, confirmed this observation at the same time as he told me that the *mallero* (*see above,* section on Wooden Objects) was the right size to make and repair the nets found in the excavations.

The 1983 collection of net fragments includes 18 examples (Table 16), with the majority in Complex D and the rest in Complex C (Complex B was not present in the 1983 excavation area). A much higher proportion of these net fragments were made of cotton than in the 1984 excavation sample, though vegetal fiber still predominates. The 1983 collection has a greater variety of knot types than the 1984 collection; simple and square knots account for only a third of the cases, while the other two thirds used the cowhitch knot (Fig. 45B) (Emery, 1966:35 and Figs. 27, 28). Cowhitches are generally used on the edges of nets. The three 1983 examples with simple

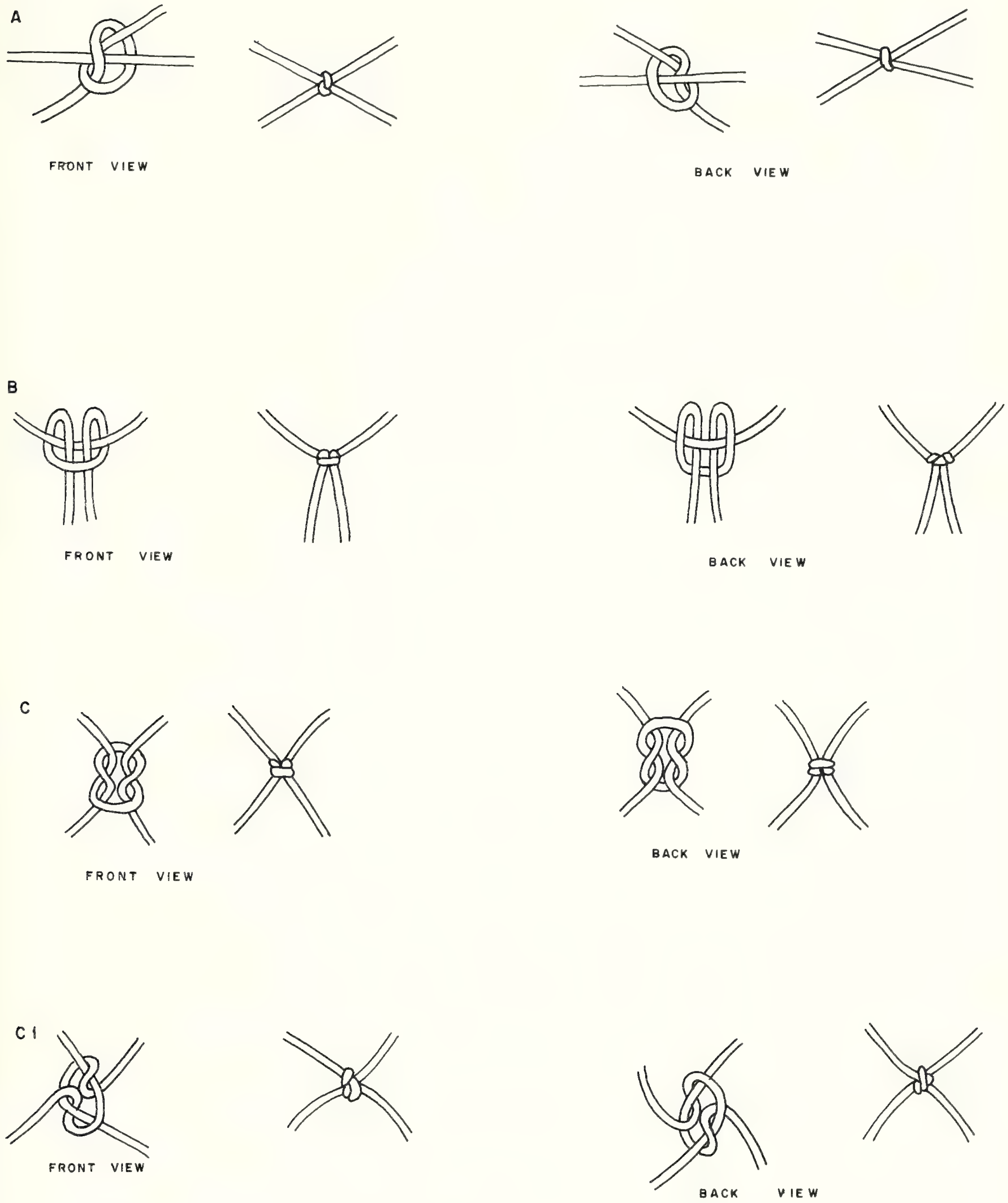

Fig. 45.—Netting knots. A) Simple knot. B) Cowhitch. C) Square knot. C1) Square knot variant.

Table 14.—*Net fragments from 1984 excavations in Sector I, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989: Appendix B); Su, subunit; SC, stratigraphic complex. Under Mat. (material): C, cotton; VF, vegetal fiber. Under Twist: z-S, Z-spun, S-plied; s-Z, S-spun, Z-plied. Thick., thickness of yarns in mm. Under Knot: A, simple knot; C and C1, square knot (two variants)* (see *Fig. 45). No. Knots, number of knots preserved on specimen. No. Mesh, number of complete, preserved meshes on specimen. Σ4, sum of four sides of complete mesh in centimeters. Data from DiAnderas (personal communication, 1985).* [a,b,d,e] *Fragments of the same net.* [c] *One example of each square knot variant.*

Cat.	Su	SC	Mat.	Twist	Thick.	Knot	No. Knots	No. Mesh	Σ4
396[a]	3A	D	VF	z-S	0.8–1.0	A	33	4	4.0
396[a]	3A	D	VF	z-S	1.0	A	4	0	
801	2C/4D	D	VF	z-S	1.5	A	1	0	
1294	4B	D	VF	z-S	1.0	A	1	0	
991	3B	C	VF	z-S	1.6	A	1	0	
991	3B	C	VF	z-S	1.6	A	1	0	
991	3B	C	VF	z-S	1.0	A	4	0	
991	3B	C	VF	z-S	1.0	A	3	0	
991	3B	C	VF	z-S	1.0	A	2	0	
991	3B	C	VF	z-S	1.0	A	2	0	
991	3B	C	VF	z-S	1.0	A	2	0	
1030	3D	C	VF	z-S	1.2–1.3	A	6	0	
1031[b]	3D	C	VF	z-S	1.0–1.3	A	39	6	6.0
1031[b]	3D	C	VF	z-S	1.0	A	6	0	
1031[b]	3D	C	VF	z-S	0.8–1.0	A	4	0	
1031[b]	3D	C	VF	z-S	1.0–1.2	A	3	0	
1031[b]	3D	C	VF	z-S	1.0	A	2	0	
1031[b]	3D	C	VF	z-S	1.0	A	2	0	
1031[b]	3D	C	VF	z-S	0.8–1.0	A	3	0	
1031[b]	3D	C	VF	z-S	1.0	A	1	0	
1031[b]	3D	C	VF	z-S	1.0–1.1	A	2	0	
1031[b]	3D	C	VF	z-S	1.0–1.2	A	5	0	
1031[b]	3D	C	VF	z-S	?	A	1	0	
1253	2A	C	VF	z-S	1.2	A	8	0	
1051	1A	B	VF	z-S	1.0	A	4	0	
1051	1A	B	VF	z-S	1.0	A	3	0	
1051	1A	B	VF	z-S	1.0	A	1	0	
1051	1A	B	VF	z-S	1.0	A	1	0	
1051	1A	B	VF	z-S	1.0	A	1	0	
1470	3B	B	VF	z-S	1.4	A	1	0	
1502	3B	B	VF	z-S	1.0	A	30	3	6.5
1502	3B	B	VF	z-S	1.0	A	10	0	
1502	3B	B	VF	z-S	1.0	A	7	1	6.0
1502	3B	B	VF	z-S	1.0	A	8	0	
1502	3B	B	VF	z-S	1.0	A	8	0	
1502	3B	B	VF	z-S	1.0	A	8	0	
1502	3B	B	VF	z-S	1.0	A	7	0	
1502	3B	B	VF	z-S	1.0	A	4	0	
1502	3B	B	VF	z-S	1.0	A	3	0	
1502	3B	B	VF	z-S	1.0	C, C1[c]	2	0	
1534[d]	3B	B	VF	z-S	1.0	A	6	0	
1534[d]	3B	B	VF	z-S	1.0	A	7	0	
1534[d]	3B	B	VF	z-S	1.0	A	4	0	
1534[d]	3B	B	VF	z-S	1.0	A	4	0	
1534[d]	3B	B	VF	z-S	1.0	A	2	0	
1534[d]	3B	B	VF	z-S	1.0	A	2	0	
1534[d]	3B	B	VF	z-S	1.0	A	3	0	
1534[d]	3B	B	VF	z-S	1.0	A	4	0	
1534[d]	3B	B	VF	z-S	1.0	A	2	0	
1534	3B	B	VF	z-S	1.0	A	4	0	
1534	3B	B	VF	z-S	1.2	A	1	0	
1535	3B	B	VF	z-S	1.3	A	4	0	
1535	3B	B	VF	z-S	1.3	A	2	0	
1562	3D	B	VF	z-S	1.6–1.7	A	2	0	

Table 14.—*Continued.*

Cat.	Su	SC	Mat.	Twist	Thick.	Knot	No. Knots	No. Mesh	Σ4
1565	3D	B	VF	z-S	1.6	A	2	0	
1742[c]	2B	B	C	z-S	0.9–1.6	A	54	29	4.0
1742[c]	2B	B	C	z-S	0.9–1.6	A	47	20	4.0
1766	2B	B	VF	z-S	1.8	A	2	0	
1766	2B	B	VF	z-S	1.3	A	1	0	
1768	2B	B	VF	z-S	1.0	A	4	0	
1768	2B	B	VF	z-S	1.0–1.5	A	3	0	
1768	2B	B	VF	z-S	1.5	A	2	0	
1768	2B	B	VF	z-S	1.0	A	1	0	
1768	2B	B	VF	z-S	1.3	A	1	0	
1804	4B	B	C	s-Z	2.0	A	1	0	
1804	4B	B	C	s-Z	2.0	A	1	0	
1812	2D	B	VF	z-S	0.8–1.0	A	1	0	
1813	2D	B	VF	z-S	0.8–1.0	A	1	0	

Summary by Stratigraphic Complex

Complex D: three fragments from two different nets; all simple knots, all vegetal fiber, all Z-spun, S-plied; one example with whole mesh, Σ4 sides = 4.0 cm.

Complex C: 20 fragments from ten different nets; all simple knot, all vegetal fiber, all Z-spun, S-plied; one example with whole mesh, Σ4 sides = 6.0 cm.

Complex B: 44 fragments from 35 different nets; 43 fragments with simple knot, one fragment with two variants of square knot; 40 fragments of vegetal fiber and Z-spun, S-plied yarns; four fragments of cotton, two with S-spun, Z-plied yarns and two with Z-spun, S-plied yarns; four examples with whole mesh, Σ4 = 6.5 cm, 6.0 cm, and 4.0 cm (two examples from same net).

knots were made of vegetable fiber, while the other two knot types included both vegetal fiber and cotton examples.

The context and nature of the net fragment occurrences in Lo Demás Sector I are consistent with a traditional pattern of net use still employed in Tambo de Mora. On days or at times when they are not fishing, the fishermen sit on the street in front of their houses repairing their nets with a tool kit that includes *malleros* (Fig. 46). Each broken segment of net is excised and discarded in the street. The result is an accumulation of net fragments with

Table 15.—*Traditional net measurements from Peru, adapted from Coker (1908–II, 1980–VII). Plana, Cuadrada, and Σ4 Sides are measured in cm. Names of the nets refer to the fish species for which they are intended. The information on all nets except the* anchovetera *is from a table (Coker, 1908–II:58) for gill nets. The line in the table for the* anchovetera *net is drawn from a later section of Coker's work (1908–VII:105), in which he describes an* anchovetera *from the Chilca area as having a mesh of "1½ centímetro (3¼ centímetros el cuadrado) y menos." Because the first measurement must be plana (the only measurement in cm used by Coker other than cuadrado), the cuadrado measurement must mean "three quarters." Coker describes the* anchovetera *as a very small mesh "chinchorro" (beach seine with wings and bunt, Spoehr, 1980:23) used from canoes.*

Name	Dedo	Plana	Cuadrada	Σ4 Sides
anchovetera	?	1.5	0.75	3
pejerreyera	1	3–4	1.5–2	6–8
cabincera	3	6	3	12
licera/bonitera	4	8–10	4–5	16–20
bonitera corvinera	7	14–15	6.5–7.5	28–30
corvinera	8	12–18	8–9	32–36
robalera	9	18–20	9–10	36–40

Table 16.—*Net fragments from the 1983 excavations in Sector I, Lo Demás. Data from Fattorini (1984). Abbreviations: Complex, stratigraphic complex in Sector I; Cat., catalogue number (Sandweiss, 1989:Appendix B). Under Material: C, cotton; VF, vegetal fiber. Under Knot Type: A, simple knot; B, cow hitch; C, square knot (*see *Fig. 45).*

Cat.	Subunit	Complex	Material	Knot Type
14	A2	D	C	C
17	A1	D	VF	B
17	A1	D	VF	B
17	A1	D	VF	B
18	A2	D	VF	C
19	A2	D	VF	?
19	A2	D	C	B
20	A2	D	C	A
20	A2	D	C	A
20	A2	D	C	A
22	A1	D	VF	B
37	C3	D	A	B
42	B3	D	VF	B
44	B3	C	C	B
48	A1	C	VF	C
48	A1	C	C	B
52	A2	C	VF	A
113	B3	C	VF	B

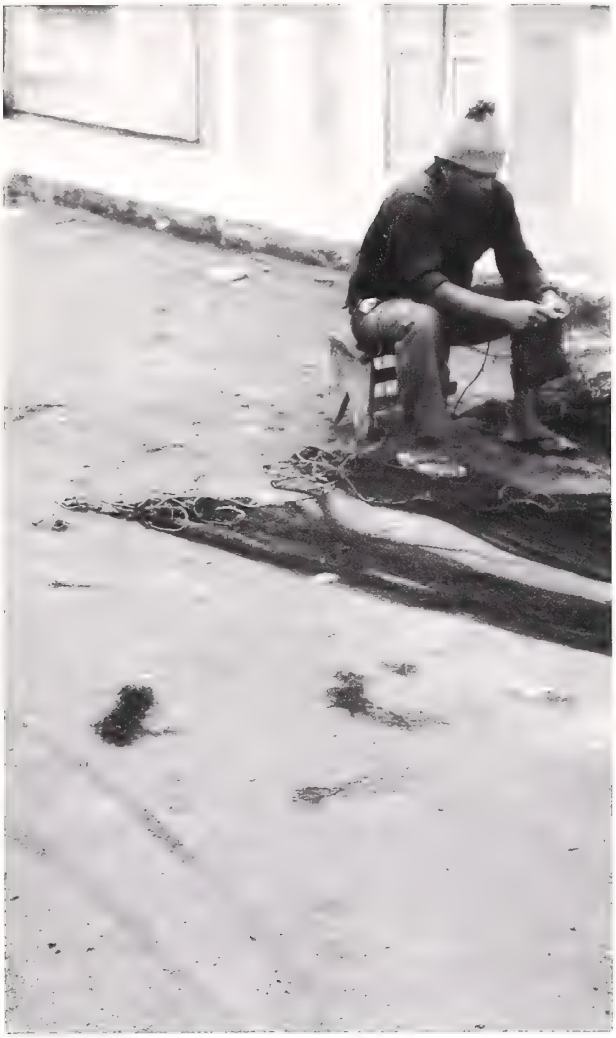

Fig. 46.—Fisherman repairing nets in the principal street of Tambo de Mora, 1984. Note excised net fragments discarded in the street.

few whole meshes, similar to the net fragments from the excavations at Lo Demás.

TEXTILES

Textile fragments and especially threads were a common constituent of the excavated deposits at Lo Demás. Thus far, only the sample from the 1983 excavation in Sector I has been studied in detail (Fattorini, 1984); observations on the 1984 sample consist only of noting the presence of at least one complete piece, an undecorated belt, and a number of fairly large fragments in addition to the usual small fragments and threads. Studies on the woven items in the Uhle Chincha collection (O'Neale and Kroeber, 1930; O'Neale et al., 1949; Garaventa, 1979) provide some comparative data on late pre-Hispanic Chincha textiles.

Table 17.—*Loose threads by material from 1983 excavation in Sector I, Lo Demás, by stratigraphic complex. Stratigraphic Complex B was not present in the 1983 excavation subunits (*see *Chapter 5). Data from Fattorini (1984).* [a] *Two of the wool threads were dyed red and found together in Subunit A2, level 2d, cat. 19.* [b] *Seven of the vegetable fiber threads came from the same context, Subunit A2, level 3bii, cat. 52.*

Complex	Cotton	Wool	Veg. Fiber	Total
D	59	4[a]	0	63
C	52	1	8[b]	61
A	3	0	0	3
Total	114	5	8	127

Graciela Fattorini (Instituto Nacional de Cultura, Lima) studied the textiles from the 1983 excavation at Lo Demás. The study sample consists of 127 loose threads and 42 fragments of cloth (Fattorini, 1984). Most (89.9%) of the loose threads (Table 17) and all but one of the textile fragments (Table 18) are cotton. The exceptions are five wool threads, eight vegetal fibers, and one decorated wool textile fragment (Fig. 47, discussed in detail below).

All of the textile fragments in the 1983 sample from Lo Demás are plainweaves, most commonly with paired warps and single wefts (Table 18). Similarly, O'Neale et al. (1949:13) found that paired warps crossed by single wefts characterized the majority of specimens (62 out of 112) in the sample of late pre-Hispanic Chincha textiles excavated by Uhle.

Selvages are present on ten of the Lo Demás specimens. Four fragments have stitches, either where the pieces had been attached to other cloths or where rips had been mended. Three specimens have patches. O'Neale et al. (1949:141) found 11 patched specimens in the Uhle Chincha collections; they note that the "standards [of the mender] were much below those held by the weaver." Fattorini (1984) makes a similar observation concerning the Lo Demás patched textiles.

The only textile made of wool (both warps and wefts) is also the only decorated cloth from the 1983 collection (Fig. 47; Table 18:cat. 84). Torn on three sides, this fragment is a weft-faced plainweave with a chained warp selvage on the one untorn edge (M. Young, personal communication, 1988). Decoration consists of weft stripes in red, blue-purple, and

Table 18.—*Textile fragments from 1983 excavation in Sector I, Lo Demás. Data from Fattorini (1984). Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex. Under Mat. (material): C, cotton; W, wool. Wp, warp; Wf, weft. Dimensions in cm.*

Cat.	SC	Mat.	Dimensions	Wp/cm^2	Wf/cm^2	Remarks
7	D	C	2.0 × 3.1	27	16	warp-predominant plainweave
9	D	C	6.5 × 4.8	19	11	warp-predominant plainweave
12	D	C	1.6 × 2.2	11	14	plainweave
13	D	C	1.6 × 2.5	19	16	plainweave
15	D	C	4.3 × 1.6	14	23	plainweave
17	D	C	5.8 × 3.3	24	11	warp-predominant plainweave
17	D	C	6.1 × 3.0	25	14	warp-predominant plainweave
17	D	C	15.8 × 11.5	27	14	warp-predominant plainweave
17	D	C	30.0 × 15.5	27	14	semi-basket plainweave, 1 selvage, loom cords
19	D	C	2.6 × 6.8	32	13	warp-faced plainweave, 1 selvage
19	D	C	2.6 × 6.2	33	16	warp-predominant plainweave
20	D	C	19.8 × 32.0	29	16	warp-predominant plainweave w/stitching
22	D	C	45.0 × 20.0	29	16	warp-predominant plainweave, 2 selvages
31	D	C	5.3 × 7.0	18	14	plainweave
32	D	C	4.8 × 5.7	23	12	warp-predominant plainweave
43	D	C	2.8 × 2.7	7	15	weft-predominant plainweave
43	D	C	29.3 × 25.0	24	11	warp-predominant plainweave, 2 selvages, patches and stitching
71	D	C	2.5 × 1.2	18	6	warp-predominant plainweave
79	D	C	1.7 × 0.8	18	7	semi-basket plainweave
82	D	C	4.4 × 2.0	?	?	plainweave
93	D	C	12.0 × 13.7	19	14	warp-predominant plainweave, 1 selvage, stitching along 1 edge
94	D	C	8.5 × 2.6	12	8	warp-predominant plainweave
94	D	C	5.4 × 4.7	20	14	warp-predominant plainweave, 1 selvage
27	C	C	3.5 × 4.7	21	13	warp-predominant plainweave, 1 stitch
44	C	C	5.6 × 10.3	29	17	warp-predominant plainweave
45	C	C	7.2 × 3.0	26	12	warp-predominant plainweave
46	C	C	2.3 × 1.9	11	8	plainweave
48	C	C	3.6 × 2.1	14	9	plainweave
51	C	C	2.9 × 2.7	27	20	plainweave
52	C	C	6.8 × 7.5	21	12	warp-faced plainweave, 1 selvage, stitching
52	C	C	9.3 × 13.0	40	27	warp-predominant plainweave, 1 selvage
54	C	C	4.7 × 4.3	20	38	weft-predominant plainweave, 1 selvage, 2 patches
59	C	C	14.0 × 9.8	30	17	warp-predominant plainweave, 1 selvage w/paired warps, 4 patches
84	C	W	14.5 × 3.6	14	26	weft-faced plainweave w/chained warp selvage, decorated w/stripes in red, blue-purple, and yellow on brown
91	C	C	4.8 × 2.6	?	?	plainweave
91	C	C	2.1 × 1.5	?	?	plainweave
91	C	C	2.0 × 2.4	?	?	plainweave
91	C	C	2.5 × 4.5	?	?	plainweave
91	C	C	2.6 × 4.1	?	?	plainweave
91	C	C	2.2 × 3.5	?	?	plainweave
101	C	C	5.9 × 2.0	20	14	warp-predominant plainweave
131	A	C	4.9 × 7.4	25	14	warp-faced plainweave, 1 selvage

yellow on a brown background. Striping is the "only colored decoration on the Chincha domestic cloths" from the Uhle Chincha collections (O'Neale et al., 1949:141). According to O'Neale et al. (1949:142),

> "No specimen in the Chincha plain-weave group has stripes showing more than three colors, exclusive of the color of the ground material. The ground color is usually neutral and may originally have been white or brown. The most frequently occurring color in the stripes is brown, followed by blue. Red and rose occur only twice."

The striped wool textile from Lo Demás fits this description quite well, especially if the yellow stripe may be considered as light brown.

O'Neale et al. (1949) deal only with the cotton plainweaves, and they do not differentiate their sample chronologically by associated ceramics; thus, their

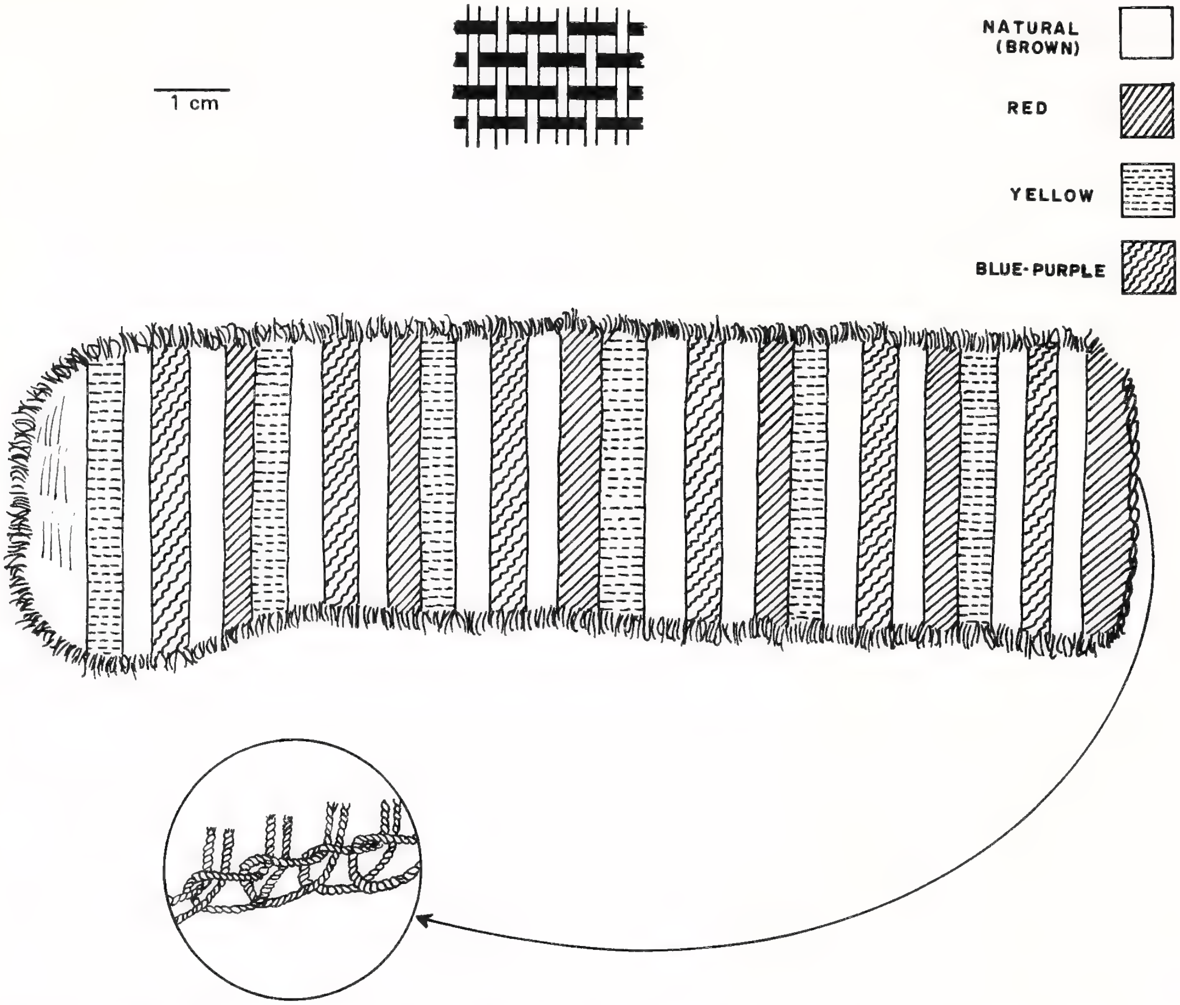

Fig. 47.—Striped, wool textile fragment, weft-faced plainweave with chained warp selvage, from Lo Demás, Sector I, Subunit A2, feature 18a, Stratigraphic Complex C (cat. 84). *See* Table 18.

textile study does not aid in analyzing the wool piece from Lo Demás. Garaventa (1979) does describe wool textiles from the Uhle Chincha collections, although her sample includes only those specimens from graves assigned to Menzel's (1966) Chincha style (Late Intermediate Period 8/early Late Horizon). Four of the 13 textiles studied by Garaventa are made entirely of wool, while others have a wool warp or weft, or wool brocading. The all-wool pieces "include belts, a bag, and a neckpiece" (Garaventa, 1979:229). One of these specimens, a bag, is a weft-faced plainweave, like the Lo Demás wool textile (Garaventa, 1979:220, 229–230 and Fig. 7); decoration consists of stripes in four shades of brown and cream. Unlike the Lo Demás piece, the stripes on the bag vary in width. The bag comes from Uhle's (1924) Cemetery B (PV 57–6), 50 m east of Sector I of Lo Demás (*see* Figs. 1 and 3).

Until an analysis of wool textiles from the Chincha graves with Inka associations is available, the chronological significance of the Lo Demás wool fragment is limited to the observation that the piece is similar to other late pre-Hispanic examples from the same area.[76] The undecorated cotton fragments also concord with the Uhle sample of late pre-Hispanic textiles in terms of material, technique, and condition.

Spinning and Sewing Equipment

Although only two possible items of weaving equipment were found in excavations of Sectors I and IV at Lo Demás (the wooden and bone "ruqquis"), spinning and sewing equipment was fairly common, as were cotton bolls and seeds (*see* Chapter 10). Spinning implements included both spindle whorls and spindles, while sewing equipment consisted of cactus spine and bone needles. Loose threads were abundant, but most probably came from disintegrating textiles (*see above,* section on Textiles). Although several balls or shanks of thread were recovered from looters' backdirt in Sector II, we found none in Sectors I and IV. Some of the analyzed textiles from the 1983 excavations in Sector I were patched, probably at Lo Demás.

Spindle Whorls

Twenty-three whole or fragmentary spindle whorls were recovered from Sectors I and IV in Lo Demás (Table 19). Of these specimens, 19 came from Sector I (evenly distributed between Stratigraphic Complexes B to D) and four came from Sector IV. Table 19 presents provenience and hole diameter, height, and maximum width for the whorls.[77] Only six specimens are complete, so not all dimensions could be measured in all cases. Based on the available measurements, the mean whorl height is 1.29 cm (SD = 0.23 cm), the mean hole diameter is 0.37 cm (SD = 0.03 cm), and the mean maximum width is 1.46 cm (SD = 0.20 cm). For the five specimens for which all three dimensions are available, the mean ratio of height to maximum width is 0.94 (SD = 0.13), the mean ratio of hole diameter to height is 0.28 (SD = 0.04), and the mean ratio of hole diameter to maximum width (including a sixth measurement) is 0.26 (SD = 0.06). In qualitative terms, the Lo Demás spindle whorls tend to be roughly spherical with a cylindrical hole about one quarter the diameter of the sphere. Only one specimen, a painted fragment from Sector IV, has any decoration (Table 19:cat. 1765).

Table 19.—*Spindle whorls from excavations in Sectors I and IV, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex (Sector I); Lv, Level (Sector IV, Subunit 26D); Hole D., hole diameter; Max. Width, maximum width. Under Condition: W, whole; ~W, mostly whole; F, fragment. A question mark indicates that a measurement could not be taken because of poor preservation. Measurements are in cm.* [a] *Still attached to spindle;* see *Table 20: cat. 1028.* [b] *Pulverized.* [c] *Painted.* [d] *Broken in two.*

Cat.	SC	Lv	Hole D.	Height	Max. Width	Condition
			Sector I			
550	D		?	1.4	?	F
561	D		0.4	1.3	1.4	W
567	D		0.4	1.3	1.1	W
829	D		0.4	?	?	F
1069	D		?	1.3	?	F
1254	D		?	?	?	F
872	C		?	1.1	?	F
1074	C		0.4	?	1.5	~W
1082	C		?	?	?	F[a]
1104	C		?	1.6	?	F
1215	C		?	1.4	?	F
1408	C		0.4	1.2	1.5	W
1500	C		?	1.2	?	F
1089	B		?	1.3	?	F
1120	B		?	1.4	?	F
1352	B		?	1.4	?	F
1389	B		0.4	1.5	1.7	W
1797	B		?	?	?	F[b]
1855	B		?	?	?	F
			Sector IV			
1765		7b	?	?	?	F[c]
1851		13b	0.3	1.5	1.5	W[d]
1854		15	?	1.0	?	F
1874		17	?	?	?	F

Uhle (1924) recovered a number of spindles and whorls from late pre-Hispanic graves in Chincha. Kroeber and Strong (1924:32–33 and Plates 16–18) briefly discuss and illustrate these artifacts, dividing them into Late Chincha I and Late Chincha II/Inka types based on associated diagnostic pottery and other artifacts. The Lo Demás spindle whorls fit the description of Late Chincha I (= pre-Inka Chincha style, Menzel, 1966) form as "more or less spherical" (Kroeber and Strong, 1924:32); the Late Chincha II/Inka types have varied forms but are "rarely spherical" (Kroeber and Strong, 1924:33). However, the Late Chincha I whorls tend to be made of highly polished black pottery, usually incised and sometimes painted, while the Late Chincha II/Inka whorls are "made of very poorly baked pottery, unpolished and not incised [and a] number of them have split or crumbled off the spindle" (Kroeber and Strong, 1924:32–33). The Lo Demás whorls are closer to the Late Chincha II/Inka types in that they are often broken, are not incised, and are not blackware. The combination of Late Chincha I form and Late Chincha II/Inka manufacture suggests a synthesis of the two traditions, and further supports the Late Horizon date for Lo Demás.

Needles and Spindles

We recovered 38 whole or fragmentary needles and spindles from excavations in Sectors I and IV of Lo Demás, 26 from Sector I and 12 from Sector IV (Table 20). All but four of the specimens are made of cactus spine; the exceptions are three bone needles and one wooden object which may be a spindle.

Differentiating between needles and spindles often presented a problem, given the fragmentary nature of most specimens. Both classes of artifacts are long and relatively narrow. Needles and spindles

Table 20.—*Needles and spindles from excavations in Sectors I and IV, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC/lv, stratigraphic complex (Sector I)/ level or feature (Sector IV); Max. Width, maximum width. Under Material: cactus, cactus spine. Under Part: N, complete needle (with point and hole); NFH, needle fragment with hole; NFP, needle fragment with point; NF, needle fragment without hole or point; SFP, spindle fragment with point; SF, spindle fragment without point; +C, ceramic around shaft (probably broken whorl); +P, painted. All measurements are in cm.* [a] *Broken at the hole.* [b] *This specimen is cylindrical, with the center carved out, several hairs wrapped around one end, and dark thread around the other. If it is a spindle, it is unlike the others found in Lo Demás and in the graves excavated by Uhle (1924; Kroeber and Strong, 1924).* [c] *This specimen has several areas of red paint.* [d] *This specimen has traces of pink paint.*

Cat.	SC/lv	Length	Max. Width	Material	Part
		Sector I			
343	D	2.9	0.1	cactus	NFP
370	D	2.0	0.3	bone	N
440	D	6.9	0.1	cactus	NFP
480	D	3.0	0.1	cactus	NFH
527	D	8.1	0.2	cactus	NFP
600	D	4.3	0.1	cactus	NF
600	D	5.0	0.1	cactus	NFP
700	D	3.5	0.1	cactus	NFH
829	D	5.5	0.2	cactus	NFP
929	D	6.0	0.3	cactus	SFP
995	D	5.7	0.2	cactus	NF
1260	D	2.5	0.1	cactus	NFP
484	C	5.1	0.2	cactus	NFP
837	C	5.2	0.1	cactus	NFH
837	C	5.8	0.1	cactus	NFP
858	C	4.0	0.1	cactus	NFP
872	C	2.9	0.1	cactus	NFH[a]
1028	C	9.5	4.0	cactus	SFP+C
1055	C	7.6	0.1	cactus	NFH
1425	C	16.0	0.7	wood	SF(?)[b]
1608	C	8.4	0.1	cactus	NFP
1391	B	8.3	0.4	cactus	SF+P[c]
1534	B	5.5	0.1	cactus	N
1683	B	9.7	0.4	cactus	SFP
1819	B	3.7	0.2	cactus	NFP
1847	B	3.4	0.2	cactus	NFP
1681	2	6.0	0.1	cactus	NFP
1739	5ci	14.1	0.5	cactus?	SFP+P[d]
1743	5c	4.6	0.1	cactus	NFP
1765	7b	4.2	0.2	cactus	NF
1788	f.2603i			bone	N
1800	10	3.5	0.2	cactus	NFP
1839	12d	3.4	0.2	cactus	NFP
1851	13b	7.0	0.2	bone	NFP
1851	31b	12.6	0.1	cactus	NFP
1854	15	3.0	0.2	cactus	NF
1854	15	4.5	0.3	cactus	SF
1854	15	11.0	0.3	cactus	SF

both have at least one pointed end, but only needles have holes. All six specimens with holes are only one mm in maximum width, so narrow width is potentially diagnostic of needles. Spindles must be wide enough at their maximum width so that the whorl will not fall off. Whorls from Lo Demás average 0.4 cm in hole diameter, with the smallest hole measuring 0.33 cm. Therefore, it is reasonable to assume that spindles at Lo Demás should have a maximum width greater than 0.3 cm. Whereas this criterion serves to indicate that all *complete* specimens with a maximum diameter of 0.3 cm or less are probably not spindles, it is of limited utility in assigning function to the fragments from the Lo Demás excavations. Conversely, however, widths equal to or greater than 0.3 cm would be awkward for needles, and most specimens—even fragmentary—fitting this description are probably spindles. In fact, the three specimens from Lo Demás which can be identified as spindles using other criteria measure 0.4 or 0.5 cm in maximum width. Therefore, I have tentatively classified all specimens with a maximum width of 0.3 cm or greater as spindles and those with an average width of less than 0.3 cm as needles (Table 20) (*see* Sandweiss, 1989:340, footnote 191).

I can identify three specimens as definite spindles due to the presence of an eroded spindle whorl on one (Table 20:cat. 1028, Sector I, Stratigraphic Complex C) and paint on the other two (Table 20: cat. 1391, Sector I, Complex B; cat. 1739, Sector IV, Subunit 26D, level 26–5ci). Kroeber and Strong (1924:32) describe Late Chincha I spindles from Uhle's Chincha collections as "painted little or not at all," while the "Inca spindle . . . normally has some 7 or 8 cm. of its middle length painted, sometimes in as many as five colors: yellow, green or blue, white, black, and red." The presence of red and pink pigment on the two specimens from Lo Demás fits the later, Inka tradition.

Four of the specimens covered in this section require further discussion. The bone needles from Sector I, Stratigraphic Complex D (Fig. 48a and Table 20:cat. 370) and from feature 2603i in Subunit 26D, Sector IV (Fig. 48b and Table 20:cat. 1788) could not have been used for ordinary cloth—the epiphyses are too wide. These specimens may have been used as netting needles. The presence of a bone object resembling a *mallero* in the same provenience (Fig. 52 and Table 24:cat. 1788) as the Sector IV bone needle supports the netting needle interpre-

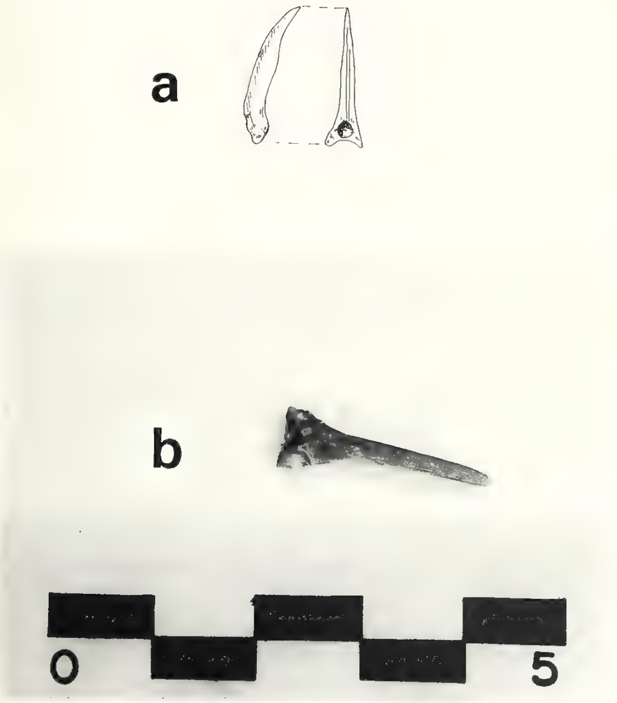

Fig. 48.—Bone needles from Lo Demás. a) From Sector I, Subunit 2D, feature 213, Stratigraphic Complex D (cat. 370). Scale is 1:1. b) From Sector IV, Subunit 26D, feature 2603i (cat. 1788). See Table 20.

tation. The other bone needle from Subunit 26D, level 26–13b (Table 20:cat. 1851) is long, slender, and slightly curved. This object would work well as a cloth needle.

The wooden object from Sector I, Stratigraphic Complex C (Table 20:cat. 1425) is certainly not a needle and may not be a spindle, either. This specimen is cylindrical and relatively wide; the center is carved out, a dark line circles one end, and a few hairs are wrapped around the other end. Both ends appear broken, and I can assign no function to this piece.

Despite the problems in distinguishing between needles and spindles in many cases, the definite identification of some examples in each of these artifact categories indicates that both spinning and sewing took place at Lo Demás. Definite spindles are present in both Sector I and Sector IV; although definite needles were not found in Sector IV, the curved bone almost certainly served that function, and several of the other specimens from this sector are sufficiently long and narrow to be classified as needles. Thus, both spinning and sewing took place in both the common and elite sectors of the site. To the degree that some of the spindles fit Kroeber and Strong's (1924:32) definition of Inka period spindles, this artifact category supports the analyses of other materials which indicate that the Uhle collections do not contain two chronologically distinguishable units.

SANDAL

One piece of footgear, a sandal, was recovered from Stratigraphic Complex D in Sector I (Fig. 49). The sole is made of coiled vegetal fiber rope. The sole has a maximum width of 12.5 cm near the toe and tapers towards the heel to a width of 8.5 cm. The maximum length is 18 cm, but the heel is worn out, and the original length was somewhat greater. The straps are made of braided wool yarns of tan-yellow, dark brown, and what seems to have been a dark blue.

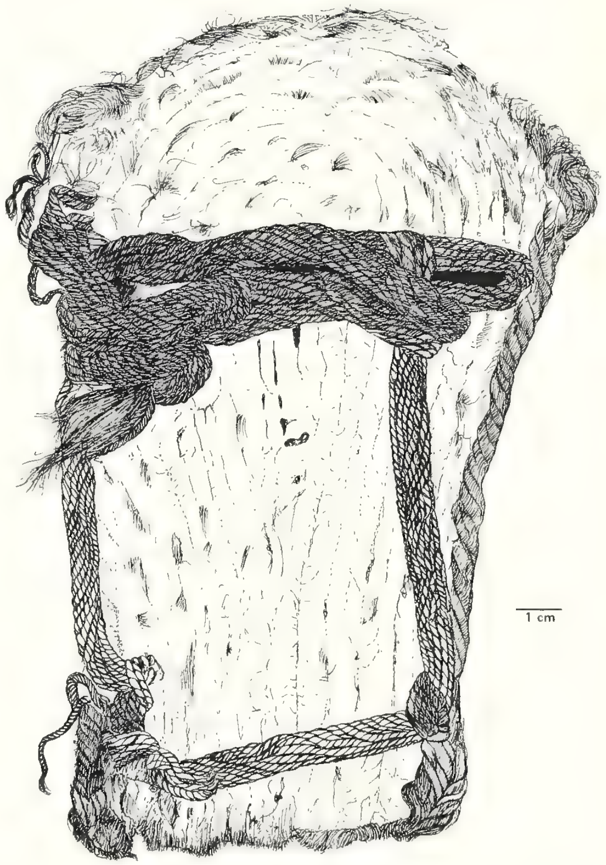

Fig. 49.—Vegetal fiber and wool cord sandal from Lo Demás, Sector I, Subunit 4C, level 7i, Stratigraphic Complex D (cat. 1069).

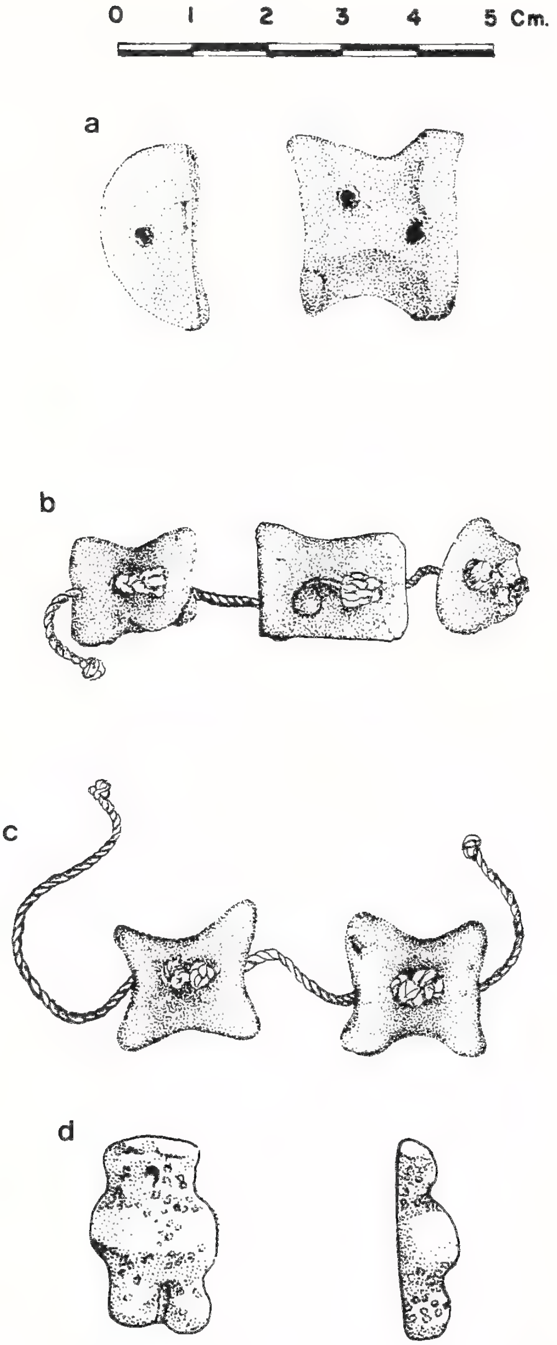

Fig. 50.—Half-bobbin objects made of clay. a) From the Ranchería site (PV 57–14) near Lurinchincha (*see* Fig. 1). b) and c) From Lo Demás, Sector IV, Subunit 26D, level 5 (cat. 1726). d) From Lo Demás, Sector IV, Subunit 26D, level 13 (cat. 1841). See Table 21 for b, c.

Mejía Xesspe (1975–1976:30–31 and Figs. 6 and 7) describes this type of sandal, his Type E, as

> "the true *llanke* that was used among the peoples of the coast and the interandean valleys. The material used for the llanke was cotton and *maguey* or *cabuya* yarns and cords. The straps were of the same material or in some cases of polychrome wool yarn, particularly for feminine use."

Of the two *llankes* illustrated by Mejía Xesspe, one (Mejía Xesspe 1975–1976:Fig. 6) is nearly identical to the Lo Demás sandal. This specimen was excavated by Max Uhle in 1906 from a late pre-Hispanic grave in the Rinconada de Ate site, Lima valley (Mejía Xesspe, 1975–1976:31). All of the archaeological examples of footgear from Peru (representations as well as the actual objects) discussed by Mejía Xesspe (1975–1976:28, 33, 37–38) date to the Late Horizon. His analysis of the drawings of Guaman Poma de Ayala found two types of footgear represented; of these, one is the *llanke,* seen only in association with people of Inka affiliation (Mejía Xesspe, 1975–1976:37).

The "Aviso" document lists *zapateros* (shoemakers) among the artisans of the Inka empire; some made very fine footgear specially for the Inka. However, these *zapateros* made their products of leather rather than fiber ("Aviso," Rostworowski, 1970: 168). Rostworowski (1977:245) mentions both shoemakers ("alpagateros") and sandalmakers for the north coast (*see* Chapter 2).

In his excavations at Chincha, Max Uhle found one rawhide sandal and "6 pairs of sandals, woven, twined, or sewn 5-strand braid" (Kroeber and Strong, 1924:51). Unfortunately, all of these examples came from the Huaca de Alvarado (PV 57–10, *see* Fig. 1), a late Formative Period structure with intruded Chincha style and post-Chincha assemblage graves; even in 1901, looting had disturbed the burials so much that the exact affiliation of any material could not be determined.

HALF-BOBBIN OBJECTS

A test pit in the Ranchería site (PV 57–14), dug in March of 1984, produced several specimens of an unusual artifact type shaped like half-bobbins. This puzzling type had not appeared during the 1983 test excavation at Lo Demás, but 19 whole or fragmentary specimens were found there in the 1984 excavations in Sectors I and IV, and one was picked up from the surface of Sector I. An additional specimen came from the excavation in Sector II, and another from a surface collection at a bluff-top site to the north of Lo Demás (Vivanco, 1987:122). All of the "half-bobbin" objects from Lo Demás and Ranchería are made of clay, while the surface find from the Chincha bluff-top site is bone. Other specimens are reported from two late pre-Hispanic

Table 21.—*Half-bobbin objects from excavations in Sectors I and IV, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex (Sector I); Lv, level (Sector IV, Subunit 26D); Mn, minimum; Mx, maximum; Ct, center; Bs, base; H, height; W, width; L, length; Hls, holes (average diameter of preserved openings); Cd., condition (W, whole; ~W, mostly whole; F, fragment). A question mark indicates that a measurement could not be taken because of poor preservation. All measurements are in cm.* [a] *These three specimens are linked together by segments of cotton string pulled through each hole and knotted; the first of the three is mostly destroyed but still attached. Hole diameter could not be measured because the strings filled the holes.* [b] *These two specimens are linked to each other by segments of cotton string in the same way as the previous three specimens.*

Cat.	SC	Lv	Mn H	Mx H	Ct H	Mn W	Mx W	Ct W	Mn L	Mx L	Bs L	Hls	Cd.
						Sector I							
265	D		1.0	0.8	0.6	?	?	1.3	?	1.1	?	0.13	~W
593	D		0.9	0.9	0.6	1.7	1.7	1.2	1.7	1.7	1.5	0.13	W
608	D		?	?	0.8	?	?	1.4	?	?	2.0	0.18	~W
1029	C		1.1	?	?	1.6	?	?	?	?	?	0.13	~W
1427	C		1.4	?	0.8	2.3	?	1.2	?	?	?	0.15	F
1690	C		1.0	1.0	0.7	2.0	1.9	1.4	1.9	1.9	1.8	0.19	W
1690	C		1.1	0.9	0.8	1.8	1.6	1.3	1.8	1.9	1.7	0.23	W
1690	C		1.2	1.1	0.9	1.8	1.7	1.4	2.0	2.0	1.9	0.13	W
1056	B		1.1	0.9	0.7	1.7	?	1.4	?	2.0	1.9	0.20	~W
1534	B		1.1	?	?	?	?	?	?	?	?	0.14	F
1621	B		?	?	?	?	?	?	?	?	?	?	F
1767	B		?	?	?	?	?	?	?	?	?	?	F
Surface			0.9	?	0.7	1.8	1.6	1.1	?	1.3	?	0.17	~W
						Sector IV							
1726		5	?	?	?	?	?	?	?	?	?	?	F[a]
1726		5	?	?	0.7	?	?	1.3	?	?	1.8	?	W[a]
1726		5	0.8	?	?	1.5	?	?	?	?	?	?	W[a]
1726		5	1.1	1.1	0.7	1.8	?	1.2	?	1.9	1.4	?	W[b]
1726		5	1.1	1.1	0.7	1.8	1.7	1.3	1.9	1.9	1.6	?	W[b]
1737		5b	1.1	?	0.7	?	?	?	?	?	?	0.17	F
1841		13	(variant of normal model; *see* Fig. 50d)										W

coastal sites to the north and south of Chincha (*see below*).

A typical "half-bobbin" object is shaped like a spool of thread standing on one end and cut in half along a vertical plane (Fig. 50a–c). Taking the flat side as the base, the maximum basal width and length tend to be similar (Table 21). Because of the spool shape, however, the center is restricted, and the basal profile has an hourglass shape. The two lips are pierced with holes angled down from the interior to the exterior. All but one of the known "half-bobbin" specimens fit this description quite closely (Table 21); the one exception, from Subunit 26D, has a bulge in the middle rather than an indentation or waist (Fig. 50d).

In Sector I of Lo Demás, "half-bobbin" objects occurred in the three major stratigraphic complexes (B to D) as well as on the surface (Table 21). No provenience contained more than one specimen. In Subunit 26D, in Sector IV, however, we found two sets of articulated "half-bobbin" objects in a single provenience (Fig. 50b, c). These specimens show that the holes in the lips were used to link the "half-bobbin" objects together: a short piece of string was passed through each hole and knotted to keep it from slipping out, while the other end was passed through the hole of a different "half-bobbin" object. Once the string has been pulled tight, the separate, knotted strings (rather than a single line passed through all of the holes in the linked "half-bobbin" objects) keep the individual objects from sliding up and down.

The two other known occurrences of "half-bobbin" objects are at Quebrada de la Vaca, a Late Horizon shoreline site near Chala, about 300 km to the south of Chincha, and at Cerro Azul, the Late Intermediate Period/Late Horizon fishing site in Cañete, 57 km to the north of Chincha. At Quebrada de la Vaca, Trimborn (1985:40, Abb. A–1) found one bone "half-bobbin" object in a tomb; he illustrates this specimen as part of a reconstructed necklace, but there is no evidence that it was originally strung with the other pendants in the tomb. In a wrapped bundle at Cerro Azul, Kroeber (1937:252 and Plate LXXXVII–1) found "forty-three half-spools of hard, dark wood, probably huarango, tied together . . . . Each spool is a ⅔ cylinder, hour-glass notched toward the middle. Each is separately strung to the next . . . a self-knot alone keeps the string from slipping out of its hole." Although differing in material, these half-spools are identical in form and method of articulation to the "half-bobbin" objects found at Lo Demás.

The function of the "half-bobbin" objects is unknown. I have found no modern objects which resemble them, and no archaeologist (or fisherman) whom I have consulted has been able to shed any light on the matter. Not even Kroeber (1937:252) could determine the function of these artifacts, despite the fact that he had the largest collection of them; he suggested "necklace or other personal adornment?" with no great conviction. Given the regularities in form, the lack of surface treatment, and the occurrence in midden as well as burials, I do not believe that the "half-bobbin" objects were used only for ornamentation.

Although the objects themselves offer no obvious clues to their function, the sites in which "half-bobbin" objects have been found suggest the range of possible uses. This artifact type occurs in late pre-Hispanic sites close to the shore and, in the cases of Lo Demás and Cerro Azul (Marcus, 1987*a*, 1987*b*; Kroeber, 1937), in sites demonstrably occupied by fishermen in the Late Horizon. Quebrada de la Vaca is similarly Late Horizon in date (Trimborn, 1985) and is situated on a cliff overlooking the shore. Given this distribution, the "half-bobbin" objects may well have something to do with fishing. What that could have been is unclear, but if the objects had a single function, it was one that could be equally well fulfilled by ceramic, bone, or wood.

LITHICS

The inventory of lithic artifacts from Lo Demás is undistinguished by objects of fine craftsmanship, or indeed by any evidence of significant labor investment in stone tool production. I inspected the entire collection of lithic artifacts from Sectors I and IV (both seasons—1983 and 1984); artifacts and possible artifacts include a few grinding stones, part of one obsidian tool or preform of indeterminate original form, a small number of obsidian chips or waste flakes, and a large number of flakes struck from river or beach cobbles (*see* Table 22). Table 22 also includes pieces of polychaete worm calcareous heads, a grey, porous material resembling coral and referred to in Peru as "piedra pomez" (which it is not). Blocks of polychaete worm heads are often washed up on the beach, and they must have been brought to Lo Demás deliberately. Today, Peruvian coast-dwellers use this material for abrading, particularly for callouses. Topic (1982:164) refers to this material as "coral" and says that it was used as a rasp in woodworking shops at Chan Chan. In Sector I of Lo Demás, polychaete worm head fragments are concentrated in Complex B (25 in B, 5 in C, 3 in D; *see* Table 22), as are modified wood fragments (*see above* and Table 11). This correlation supports a woodworking function for the Lo Demás worm heads.

The collection of stone objects also included unmodified specimens such as intact cobbles (some from hearths or walls), cobble shatter, and pebbles of various sizes and shapes. Unmodified stones are not listed in Table 22. Some of these unmodified lithics might have been used as net weights. Such use is an old tradition in the Andes: Bird found 18 cord-wrapped stones in the Late Preceramic levels of Huaca Prieta (Bird et al., 1985:220 and Fig. 167); he interpreted these finds as possible fishing net sinkers. Wrapped stones are known from sites of various later periods along the Peruvian coast (e.g., Pozorski, 1982:188), and I have seen unmodified stones used as net weights and as anchors in the same area today.

Peter Kvietok (American Museum of Natural History) also reviewed the collection of cobble flakes from Lo Demás and selected the 13 most promising examples for edge wear analysis (Kvietok, 1988). The flakes came from cobbles composed of at least six different types of rock, all common to the Peruvian coast. Eight of the specimens (Table 23)

> "had observable use wear patterns that can be categorized into two different types. 1—Edge crushing with or without micro-step fractures that is localized to relatively few areas and is limited in areal extent. 2—Edge blunting with contiguous surface smoothing. The smoothing is often more extensive on one side of the tool than on the other" (Kvietok, 1988).

Kvietok (1988) interprets the Type 1 wear as "the result of direct hammering or crushing of the stone tool against a hard or unyielding material," while he sees Type 2 wear as "probably the result of working a pliable yet firm material in a continuous sweeping/shaving/scaling/cutting motion." The first pattern would result from working a material such as wood; a variety of wooden tools as well as some wood chips (possible wood-working debris) were found in the Lo Demás deposits (*see above*, section on Wooden Objects). The second pattern could result from scaling fish. Seven of the eight specimens

Table 22.—*Lithics from excavations in Sectors I and IV, Lo Demás. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex (Sector I); Lv, level (Sector IV, Subunit 26D); CCF, cobble cortex flake; Obs, obsidian; GrS, ground stone; PW, polychaete worm (false coral); Quz, quartz; Slt, salt chunk; s, small; m, medium; l, large; dash, not present.* [a] *Possible mano fragment.* [b] *Appears to be part of a tool or preform.* [c] *Burnt.* [d] *One large piece, five small pieces, some burnt.* [e] *One large, three small.* [f] *Three small, one medium and burnt.*

Cat.	SC	Lv	CCF	Obs	GrS	PW	Quz	Slt	Other
					Sector I				
20	D		1	—	1[a]	—	—	—	—
22	D		1	—	—	—	—	—	—
82	D		1	—	—	—	—	—	—
94	D		1	—	—	—	—	—	—
240	D		1	—	—	—	—	—	—
243	D		1	—	—	—	—	—	—
272	D		—	—	—	1-s	—	—	—
299	D		—	—	—	1-s	—	—	—
342	D		1	—	—	—	—	—	—
397	D		—	—	—	—	1-s	—	1
429	D		—	—	—	—	1-s	—	—
440	D		2	—	—	—	—	—	—
477	D		1	—	—	—	—	—	—
514	D		1	—	—	—	—	—	—
515	D		—	—	—	—	—	—	1 poss. worked cobble
553	D		1	—	—	—	—	—	—
554	D		2	—	—	—	—	—	—
561	D		—	—	—	—	—	1-m	—
577	D		—	—	—	—	—	—	1 flake (basalt?)
581	D		2	—	—	—	—	—	—
750	D		—	—	—	—	1-s	—	—
767	D		1	—	—	—	—	—	—
775	D		1	—	—	—	—	—	—
849	D		1	—	—	—	—	—	—
864	D		2	—	—	—	—	—	—
995	D		1	—	—	—	—	—	—
1068	D		—	—	—	1-s	—	—	—
1218	D		1	—	—	—	—	—	—
1254	D		—	1	—	—	—	—	—
27	C		1	—	—	—	—	—	—
48	C		1	1[b]	—	—	—	—	—
57	C		5	—	—	—	—	—	—
58	C		1	—	—	—	—	—	—
127	C		1	—	—	—	—	—	—
133	C		1	—	—	—	—	—	—
322	C		—	1-s	—	—	—	—	—
556	C		—	—	—	—	—	—	1 flake w/organics
727	C		1	—	—	—	—	—	—
730	C		1	—	—	—	—	—	—
736	C		1	—	—	—	—	—	—
747	C		—	—	—	—	1-s	—	—
762	C		—	—	—	—	—	—	1 cobble hammer
770	C		1	—	—	—	—	—	—
789	C		1	—	—	—	—	—	—
792	C		2	—	—	—	—	—	—
799	C		1	—	—	—	—	—	—
810	C		1	—	—	—	—	—	—
819	C		—	—	—	1-s	—	—	—
825	C		1	—	—	—	—	—	—
838	C		—	—	—	1-s	—	—	—
839	C		1	—	—	—	—	—	—
844	C		1	—	—	—	—	—	—
855	C		1	—	—	—	—	—	—

Table 22.—*Continued.*

Cat.	SC	Lv	CCF	Obs	GrS	PW	Quz	Slt	Other
872	C		—	—	—	—	—	—	1 pebble w/salt and red stain
877	C		—	—	—	—	—	—	1 basalt? fragment
904	C		1	—	—	—	—	—	—
911	C		1	—	—	—	—	—	—
917	C		4	—	—	—	—	—	—
932	C		1	—	—	—	—	—	—
953	C		1	—	—	—	—	—	—
955	C		1	—	—	—	—	—	—
957	C		1	—	—	—	—	—	1 angular rock w/red pigment
988	C		—	—	—	1-l	—	—	—
991	C		1	—	—	—	—	—	—
993	C		1	—	—	—	—	—	—
1003	C		1	—	—	—	—	—	—
1045	C		2	—	—	—	—	—	—
1055	C		1	—	—	—	—	—	—
1057	C		—	—	—	—	1-s	—	—
1146	C		1	—	—	—	—	—	—
1215	C		—	—	—	1-l	—	—	2 poss. cobble hammers
1373	C		1	—	—	—	—	—	—
1396	C		—	—	—	—	—	—	1 angular rock w/red pigment; 1 basalt? flake
1418	C		—	—	—	—	—	—	1 basalt? flake
1425	C		1	—	—	—	—	—	—
1426	C		—	—	—	—	1-s	—	—
1512	C		1	—	—	—	—	—	—
1529	C		—	—	—	—	—	—	1 cobble half, battered on unbroken end
1630	C		—	—	—	—	1-s	—	—
1664	C		—	—	—	—	5-s	—	1 flake
1690	C		—	—	—	—	1-s	—	—
1736	C		—	—	—	—	—	—	1 cobble tool (hammer?)
1746	C		—	—	—	—	—	—	1 small flake
1747	C		—	—	—	1-s	—	—	—
1025	B		1	—	—	—	—	—	—
1052	B		—	—	—	—	—	—	1 cobble hammer
1067	B		1	—	—	—	—	—	—
1077	B		1	—	—	—	—	—	—
1191	B		2	—	—	—	—	—	—
1192	B		1	—	—	—	—	—	—
1201	B		—	—	—	—	—	—	1 broken cobble w/bulb of percussion
1278	B		1	—	—	—	—	—	—
1280	B		—	—	—	—	—	—	1 basalt flake w/bulb of percussion
1324	B		—	—	—	1-s	—	—	1 medium cobble fragment missing 2 flakes
1336	B		—	—	—	—	1-s	—	—
1348	B		1	—	—	—	—	—	—
1350	B		1	—	—	—	—	—	—
1352	B		1	—	—	—	—	—	—
1361	B		1	—	—	—	—	—	—
1390	B		—	—	—	—	—	—	1 basalt flake
1391	B		5	—	—	—	—	—	—
1422	B		3	—	—	—	1-s	—	—
1470	B		1	—	—	—	—	—	—
1471	B		—	—	—	1-l[c]	—	—	—
1502	B		5	—	—	1-s	—	—	1 cobble cortex chunk
1534	B		—	—	—	—	—	—	1 small basalt? flake
1555	B		—	—	—	1-s	—	—	—

Table 22.—*Continued.*

Cat.	SC	Lv	CCF	Obs	GrS	PW	Quz	Slt	Other
1558	B		1	—	—	—	—	—	1 poss. cobble tool
1567	B		1	—	—	—	—	1-s	—
1702	B		—	—	—	—	1-s	—	—
1719	B		—	—	—	1-s	—	—	1 flake
1731	B		1	—	—	—	—	—	—
1732	B		1	—	—	—	—	—	—
1740	B		1	—	—	1-s	—	—	—
1749	B		—	—	—	2-l	—	—	1 pebble tool
1750	B		—	—	—	1-l	—	—	1 flake; 1 unifacially worked stone
1759	B		—	—	—	—	—	—	1 flake
1760	B		—	—	—	—	—	—	2 flakes
1766	B		—	—	—	—	—	—	1 flake
1769	B		—	—	—	1-s	—	—	—
1784	B		—	—	—	—	—	—	1 flake
1786	B		—	—	—	6[d]	—	—	—
1802	B		—	—	—	—	1-s	—	—
1804	B		—	—	—	—	—	—	1 flake
1814	B		—	—	—	—	—	—	1 flake
1819	B		—	—	—	1-s	—	—	—
1836	B		—	—	—	1-l	—	—	—
1837	B		—	—	—	—	1-s	—	1 flake
1850	B		—	—	—	1-l	—	—	—
1857	B		—	—	—	4[e]	—	—	—
1855	B		—	—	—	1-s	—	—	—
1859	B		—	—	—	1-m	—	—	—
1871	A		—	—	—	—	—	—	1 flake
						Sector IV			
1719		4	—	—	—	1-s	—	—	—
1720		4b	—	—	—	4[f]	—	—	—
1725		4c	1	—	—	—	—	—	—
1800		10	—	—	—	1-l	—	—	—
1841		13	—	—	—	—	—	—	1 flake
1851		13b	—	—	—	—	—	—	1 core fragment

with use wear exhibited a clear or probable Type 2 pattern; only one specimen had a Type 1 pattern (Table 23). One of the tools with Type 2 wear (Table 23:cat. 133, Stratigraphic Complex C) still had fish scales adhering to it (Kvietok, 1988).

Donnan and Moseley (1968) interpret a lithic assemblage from the Late Intermediate Period Loma Lasca site (Santa valley, north coast) as a fish processing kit. The assemblage consisted primarily of fine-grained basalt flakes, but also included several quartzite and porphyry examples. Fish remains constituted the most abundant item in the midden. The authors conclude that

> "the flakes were utilized for the scaling and cleaning of fish. Their thin sharp edges would have been ideal for the task. No other object was encountered that could have served this purpose, nor was any other item found at Loma Lasca that would have necessitated the use of flakes" (Donnan and Moseley, 1968:503).

This interpretation is consistent with Kvietok's analysis of the Lo Demás flakes.

The results of his analysis led Kvietok (1988) to characterize the Lo Demás lithic assemblage as an "expedient tool kit" in which "each tool had a limited use life [and] . . . may have been made or collected for the task at hand and then immediately discarded after use." The same may be said for the entire corpus of lithics from Lo Demás (Table 22). This kind of "unstructured" lithic tool kit is expectable among sedentary populations such as the Chincha fishermen; for such populations, Gero (1983:48) has argued that

> "tool versatility and conservation [characteristics of more labor-intensive retouched tools] are not selected for; common

Table 23.—*Lithics from excavations at Lo Demás analyzed for edge wear (Kvietok, 1988). All specimens are from Sector I. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex; Morph., morphology; PFC, primary flake struck from a cobble; CF, cobble fragment. See text for definition and interpretation of Types 1 and 2 edge damage.*

Cat.	SC	Morph.	Material	Edge Wear
133	C	PFC	andesitic tuff	Type 2
727	C	PFC	porphyritic andesite (possibly diorite)	Type 2
917	C	PFC	pelitic hornfels	Type 2
917	C	PFC	pelitic hornfels	Type 2
993	C	PFC	diorite	Type 2
1146	C	PFC	porphyritic diorite	Type 1
1422	B	PFC	andesite	Type 2
1470	B	CF	porphyritic andesite	Type 2

> stone is abundant. Rather, the sharpness of an unretouched edge is often desired, without worry about edge damage and resource replenishment. Stone can be and apparently is used expediently and casually when relying on common raw materials."

Cobbles are abundant in the Río Chico river bed (*see* Fig. 1) about one km south of Lo Demás, as well as in a former beach line less than half a kilometer to the west of the site. The fishermen would have passed this latter source of cobbles each time they went to the shore to fish.

BONE AND SHELL OBJECTS

The vast majority of shell and bone remains from Lo Demás pertain to the subsistence inventory of the site and are discussed in Chapter 9. This section covers shell and bone objects which have modifications related to nonsubsistence use or function.

Bone

Three bone artifacts have already been discussed in the section on needles; two appear to be netting needles and one is a cloth needle (*see* Fig. 48a, b and Table 20). We recovered three other bone artifacts from excavations in Lo Demás, two from Sector IV and one from Sector I (Table 24).

One of the Sector IV bone tools, from level 26–3 of Subunit 26D (Table 24:cat. 1717), was made on a right metacarpal of a young camelid (Fig. 51) (Altamirano, 1986). Although it could have served a variety of purposes requiring a hard, pointed implement, both Altamirano and B. Ojeda (personal communication) identified this tool as a *ruqqui,* an instrument used in weaving. The presence of a weaving tool supports the hypothesis of Sector IV textile manufacture based on the abundance of cotton remains in the Subunit 26D (*see* Chapter 10).

The second Sector IV bone tool is a flat, rectangular object (Fig. 52) from feature 2603i in Subunit 26D (Table 24:cat. 1788). Made of a fire-hardened camelid tibia, this object resembles a *mallero* (Altamirano, 1986).

The one bone tool uncovered in the Sector I excavations is a small piece of marine mammal long bone shaped into a triangle with one sharp point (Fig. 53 and Table 24:cat. 595) (Altamirano, 1986).

Table 24.—*Bone and shell artifacts from excavations at Lo Demás, Sectors I and IV. Abbreviations: Cat., catalogue number (Sandweiss, 1989:Appendix B); SC, stratigraphic complex (Sector I); Lv, level (Sector IV, Subunit 26D).* See also *Table 20 (cats. 370, 1788, 1851) for bone needles.*

Cat.	SC	Lv	Material	Description
				Sector I
595	C		bone	marine mammal long bone worked into a triangle with a sharpened point
1325	B		shell	nacar button, oval w/wavy profile along long sides, 10 × 8 × 3 mm, with two 2 mm diameter holes running the width of the object (i.e., ca. 8 mm long)
1470	B		shell	*Aulacomya ater* (mussel) valve with red pigment on both interior and exterior
				Sector IV
1717		3	bone	right metacarpal of a young camelid worked into a point; 11.6 cm maximum length
1788		f.2603i	bone	camelid tibia worked into a flat, rectangular tool measuring 2.9 × 1.1 × 0.4 cm maximum length, width, and thickness; possible *mallero*
1788		f.2603i	shell	*Aulacomya ater* (mussel) valve with yellow pigment
1788		f.2603i	shell	*Choromytilus chorus* valve with red pigment
1839		12d	shell	unidentified clam with red pigment
1839		12d	shell	*Choromytilus chorus* valve with red pigment
1863		f.2613	shell	*Spondylus* sp. circular bead, 4.5 mm diameter, 1 mm diameter hole

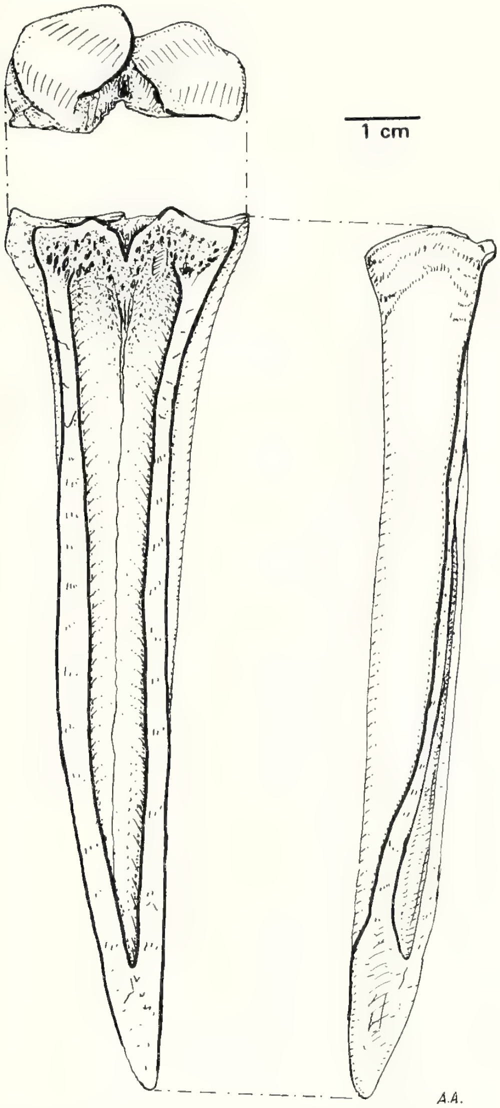

Fig. 51.—Bone *ruqqui* (weaving tool) from Lo Demás, Sector IV, Subunit 26D, level 3 (cat. 1717). See Table 24.

The function of this tool is unclear; Altamirano suggests that it could have been an awl for punching holes in leather.

Shell

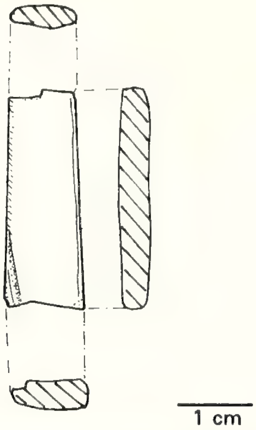

Fig. 52.—Bone *mallero* (net-making tool) from Lo Demás, Sector IV, Subunit 26D, feature 2603i (cat. 1788). See Table 24.

Excavations at Lo Demás recovered three classes of shell for or from nonsubsistence use (Table 24): a shell bead, a shell button, and painted shells. The shell button (Table 24:cat. 1325) came from Stratigraphic Complex B in Sector I. Made of nacar, this object measures approximately 10 × 8 × 3 mm, with two 2 mm diameter holes running the length of the button. The bead, of the warm water mollusk *Spondylus,* came from feature 2613, Subunit 26D, in Sector IV (Table 24:cat. 1863). This bead is circular, with a diameter of 4.5 mm; the hole in the middle has a diameter of 1 mm. Despite the fact that *Spondylus* is supposed to have been one of the major items traded by the merchants of Chincha (e.g., Rostworowski, 1970:152–153, 161), this bead is the only piece of worked *Spondylus* found in Lo Demás; unworked *Spondylus* remains consist of two bits of spine (*see* Chapter 9), one from Sector IV (feature 2612 in Subunit 26D) and one from Sector I (Stratigraphic Complex C:cat. 52).

Uhle found 12 whole *Spondylus* valves in Chincha graves, along with a fairly large number of beads and pendants made from this shell (Kroeber and

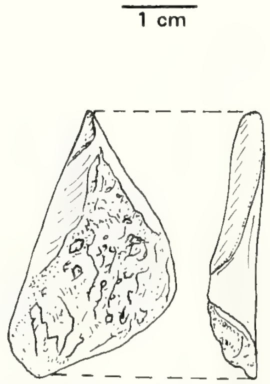

Fig. 53.—Triangular bone tool from Lo Demás, Sector I, Subunit 3C, feature 318, Stratigraphic Complex C (cat. 595). See Table 24.

Strong, 1924:30–31, 46). According to Kroeber and Strong's analysis, all of the whole valves were associated with Late Chincha II and especially Inka (= post-Chincha assemblage, Late Horizon) graves and none with the Late Chincha I (= pre-Inka) graves. Kroeber and Strong state that "spondylus and fine beads are characteristic of the Inca graves. They are virtually lacking from both LCa [Late Chincha] I and LCa II graves" (Kroeber and Strong, 1924:31). Thus, although the general lack of *Spondylus* in Lo Demás is puzzling, the location of the bead in Sector IV is consistent with other evidence that the inhabitants of this part of the site maintained close relations with the Inka.

The last, and most abundant, category of modified shells from Lo Demás are those with traces of paint (Table 24). One *Aulacomya ater* (mussel) valve with red pigment was recovered from Stratigraphic Complex B in Sector I (Table 24:cat. 1470). Two pieces of the purple mussel *Choromytilus chorus* with red pigment were found in Sector IV, Subunit 26D (Table 24:cats. 1788 and 1839); one was associated with a piece of *A. ater* with yellow pigment (Table 24: cat. 1788) and the other with a piece of an unidentified clam with red pigment (Table 24:cat. 1839). Uhle found six "mytilus" shells in his Chincha excavations, all from Late Chincha I graves (Kroeber and Strong, 1924:30). Three of these valves contained red pigment. In a brief, partial inspection of the Uhle collection in the Lowie Museum at the University of California, Berkeley, I saw that at least some of these mytilids are *Choromytilus chorus.* Although I did not see the specimens with pigment (and the curator, Lawrence Dawson, did not remember having seen them), Garaventa (1979:224) confirms the presence of three "*Mytilus*" valves with red pigment in the Uhle collection.

Choromytilus chorus occurs in nonsubsistence contexts throughout Andean prehistory, from the Lithic Period through the Late Horizon (Sandweiss, 1982:224, 1985*a*; Sandweiss et al., 1990). On the coast, the most consistent association is with red pigment, as at Chincha. What the painted valves were used for, and whether the use changed throughout the thousands of years which separate the earliest and latest occurrences, remains unclear. Because specimens often have pigment on both interior and exterior, use as paint containers is not the only answer; a more complex involvement in ritual activities is indicated.

CHAPTER 9

ORGANIC REMAINS: FAUNA

INTRODUCTION

This chapter presents and discusses the faunal remains from Lo Demás in five sections: mollusks, fish, crustaceans, vertebrates other than fish (including several miscellaneous classes), and animal coprolites. In each case, the available data represent a subsample of the excavated remains from Lo Demás; the quantity and quality of the information vary from section to section, with consequent variation in interpretations.

Fish and mollusks constitute the majority of faunal remains at Lo Demás, in accordance with expectations for a site occupied by fishermen. Among the nonfish vertebrates, seabirds and sea mammals together make up a significant proportion of the identified specimens. Although I do not attempt to calculate the exact contribution of different species to the diet of the site's inhabitants (*see below*), marine species clearly provided the bulk of the meat consumed at Lo Demás.

The faunal remains also provide data relevant to paleoenvironmental reconstruction, differential access to resources by elite and nonelite residents of the site, cross-correlation of stratigraphic complexes within and between the different sectors of the site, and patterns of capture, production, and consumption of marine animals. All of these categories of information help assess the ethnohistoric data concerning the conditions and organization of life among the Late Horizon fishermen of Chincha.

MOLLUSCAN REMAINS

Mollusks from archaeological sites offer information on topics ranging from subsistence practices and paleoenvironment to exchange networks and ritual behavior (Rollins et al., 1990). The Lo Demás mollusks provide data relevant to the reconstruction of natural and cultural features of the Late Horizon littoral environment in Chincha, as well as information on subsistence, ritual, trade, and differential access to resources by elite and nonelite residents of the site. The shells also help confirm the validity of the Sector I stratigraphic complexes originally

Table 25.—*Taxonomic list of identified mollusk species from archaeological contexts at Lo Demás (from Rodríguez, 1984, 1987).* [a] Donax obesulus *is the precedent designation of the species frequently reported in the archaeological literature as* Donax peruvianus *(see Coan, 1983:277–279).*

PELECYPODA
- Dysodontida
  - Mytilidae
    - *Semimytilus algosus* (Gould) (small mussel)
    - *Choromytilus chorus* (Molina) (large, purple mussel)
    - *Aulacomya ater* (Molina) (mussel)
    - *Perumytilus purpuratus* (Lamarck) (small mussel)
- Isodontida
  - Spondylidae
    - *Spondylus* spp. (thorny oyster, *mullu*)
  - Pectinidae
    - *Argopecten purpuratus* (Lamarck) (scallop)
  - Veneridae
    - *Eurhomalea rufa* (Lamarck) (large clam)
    - *Protothaca* (*Protothaca*) *thaca* (Molina) (medium clam)
  - Petricolidae
    - *Petricola* (*Petricola*) *denticulata* (Sowerby) (borer)
  - Mactridae
    - *Mulinia edulis* (King) (small clam)
  - Mesodesmatidae
    - *Mesodesma donacium* (Lamarck) (large wedge clam)
  - Donacidae
    - *Donax* (*Chion*) *obesulus*[a] (Reeve) (small surf clam)

GASTROPODA
- Archaeogastropoda
  - Fissurellidae
    - *Fissurella* spp. (keyhole limpets)
  - Acmaeidae
    - *Acmaea* spp. (limpets)
  - Trochidae
    - *Tegula* (*Chlorostoma*) *atra* (Lesson) (small snail)
  - Turbinidae
    - *Prisogaster niger* (Wood) (small snail)
- Mesogastropoda
  - Calyptraeidae
    - *Calyptraea* (*Trochita*) *trochiformis* (Born) (spiral limpet)
    - *Crepipatella* spp. (slipper shells)
  - Naticidae
    - *Polinices* (*Polinices*) *uber* (Valenciennes) (small snail)
- Neogastropoda
  - Thaididae
    - *Thais* (*Stramonita*) *chocolata* (Duclos) (large snail)
    - *Thais* (*Stramonita*) *haemastoma* (Linnaeus) (snail)
    - *Thais* sp. (snail)
    - *Concholepas concholepas* (Bruguière) (false abalone)
  - Olividae
    - *Oliva* (*Oliva*) *peruviana* (Lamarck) (olive shell)

POLYPLACOPHORA
- Chitonidae
  - *Chiton* spp.

OTHER
- Bulimulidae
  - *Scutalus* spp. (land snails)
- Balanidae
  - *Balanus* spp. (barnacles—Crustacea)

Table 26.—*Mollusk species from Lo Demás by potential uses. Species for which the potential use is indicated or strongly supported at Lo Demás are marked with an asterisk. Some species have more than one use (see text for details).*

Food

*Semimytilus algosus**
*Choromytilus chorus**
*Aulacomya ater**
*Perumytilus purpuratus**
Argopecten purpuratus
*Eurhomalea rufa**
Protothaca (*Protothaca*) *thaca**
*Mulinia edulis**
*Mesodesma donacium**
Donax (*Chion*) *obesulus**
Fissurella spp.*
Acmaea spp.*
Tegula (*Chlorostoma*) *atra**
*Prisogaster niger**
Crepipatella spp.*
Polinices (*Polinices*) *uber**
Thais (*Stramonita*) *chocolata**
Thais (*Stramonita*) *haemastoma**
Thais sp.*
*Concholepas concholepas**
Chiton spp.*
Scutalus spp.

Ornament

Choromytilus chorus
Spondylus spp.*
Oliva (*Oliva*) *peruviana*

Paint Container

*Choromytilus chorus**

Accidental Arrivals

*Semimytilus algosus**
Petricola (*Petricola*) *denticulata**
*Prisogaster niger**
Tegula (*Chlorostoma*) *atra**
Balanus spp.*

defined by strata orientations and architectural associations (*see* Chapter 5).

The studied sample of molluscan remains includes all of the mollusks (whole and fragments) retained in the ¼″ screen from the 1983 test excavations (Sector I), from Subunits 3B and 10D (Sector I), and from Subunit 26D (Sector IV).

María del Carmen Rodríguez H. (San Marcos University, Lima, Peru) analyzed the Lo Demás mollusks with my assistance (Rodríguez H., 1984, 1987). We identified 12 taxa of marine pelecypods (bivalves), 12 taxa of marine gastropods, one terrestrial gastropod, and chiton (*see* Table 25). Although barnacles (*Balanus* spp.) are crustaceans, we included them in the molluscan analysis because barnacles probably arrived at Lo Demás attached to rock-dwelling marine mollusks; also, like many mollusks and unlike the other crustaceans found at Lo Demás, barnacles are sessile. The sample contained a total MNI (Minimum Number of Individuals) of 13,636 and a total weight of 16,695.4 grams.

Most of the shell remains from Lo Demás came from primary midden deposits (*see* Chapter 5). Few of the shells were culturally modified except by charring, suggesting that the inhabitants of Lo Demás used mollusks principally as food (*see* Table 26).

Table 27.—*Total weight and MNI (Minimum Number of Individuals) of mollusks by taxon for all analyzed shell samples from Lo Demás (sample includes: Subunits A1, A2, A3, B3, C3, 3B, 10D in Sector I; Subunit 26D in Sector IV). MNI was aggregated by provenience. An asterisk indicates less than 0.1%. A dash means not applicable. Numbers in parentheses following MNI indicate the number of levels with fragments of a taxon but no MNI indicator; each of these levels contributed one count to the listed MNI. Data from Sandweiss (1989:Tables 33–36, 39).*

Genus/Species	Weight	%	Rank	MNI	%	Rank
Semimytilus algosus	5,407.8	32.4	2	4,875 (30)	35.7	2
Choromytilus chorus	39.8	0.2	12	46 (44)	0.3	10
Aulacomya ater	564.1	3.4	4	149 (77)	1.1	6
Perumytilus purpuratus	17.8	0.1	14	43 (17)	0.3	11
Spondylus spp.	0.2	*	26	3 (3)	*	19
Argopecten purpuratus	4.7	*	17	1 (1)	*	22
Eurhomalea rufa	1.6	*	22	1	*	22
Protothaca thaca	265.7	1.6	5	145 (81)	1.1	7
Petricola denticulata	1.7	*	21	4 (3)	*	17
Mulinia edulis	73.4	0.4	11	226 (43)	1.7	5
Mesodesma donacium	137.6	0.8	9	351 (28)	2.6	4
Donax obesulus	8,741.2	52.4	1	6,630 (13)	48.6	1
Fissurella spp.	17.3	0.1	15	13 (7)	0.1	15
Acmaea spp.	0.2	*	26	2	*	20
Tegula atra	25.3	0.2	13	101 (5)	0.7	9
Prisogaster niger	235.3	1.4	6	856 (7)	6.3	3
Calyptraea trochiformis	0.1	*	28	1	*	22
Crepipatella spp.	7.9	*	16	26 (4)	0.2	12
Polinices uber	2.6	*	20	2	*	20
Thais chocolata	721.1	4.3	3	114 (68)	0.8	8
Thais sp.	4.0	*	19	4 (2)	*	17
Concholepas concholepas	163.0	1.0	8	17 (14)	0.1	13
Oliva peruviana	0.8	*	24	1	*	22
Unidentified pelecypod	4.7	*	17	1	*	22
Scutalus spp.	1.1	*	23	17 (2)	0.1	13
Chiton spp.	0.5	*	25	7 (7)	0.1	16
Balanus spp.	84.4	0.5	10	—	—	—
Unidentified	171.5	1.0	7	—	—	—
Total	16,695.4			13,636		

However, a small number of specimens were modified in ways that indicate functions other than subsistence. Though mentioned in this chapter, the section on Bone and Shell Objects in Chapter 8 provides more detail about these specimens (*see* Table 24).

Methodology

Laboratory procedure involved several steps. First, the shell remains were washed and dried by provenience lots. Next, the remains from each provenience were separated and weighed by taxon (*see* Sandweiss, 1989:374, footnote 196). At this point, any observations on the specimens were noted (e.g., high percentage of burnt valves, presence of pigment, evidence of working). Finally, the MNI-indicators[78] were separated and the MNI counted. When identifiable fragments of a taxon found in a given provenience did not include an MNI-indicator, we assigned a default MNI of one. In compiling summary tables of the molluscan data, I included the default MNI counts in calculating total MNI.

General Characteristics of the Lo Demás Molluscan Remains

This section covers taxonomy, habitat, origin, and use of the mollusks recovered from Lo Demás. Table 25 provides a taxonomic chart of the identified mollusks. Marine gastropods and pelecypods are equally represented in number of taxa; however, the presence/absence criterion masks the real dominance of the marine pelecypods in the Lo Demás molluscan fauna (*see below* and Table 27).

Tables 28 and 29 list the habitats and geographic ranges of molluscan species from Lo Demás. In general, the Lo Demás molluscan fauna indicate littoral

Table 28.—*Mollusk species from Lo Demás by habitat (compiled from Olsson, 1961; Marincovich, 1973; Sandweiss, 1982; and Valdiviezo, personal communication).* [a] Crepipatella *spp. also occur in the subtidal zone, mostly on valves of* Aulacomya ater. [b] Concholepas concholepas *also occurs in the upper rocky subtidal zone.* [c] *The* Thais *snails are found in the lower rocky intertidal zone and both the rocky and sandy subtidal zones, where they prey on other mollusks.*

Rocky Intertidal Zone

Semimytilus algosus
Perumytilus purpuratus
Fissurella spp.
Acmaea spp.
Tegula atra
Prisogaster niger
Calyptraea (*Trochita*) *trochiformis*
Crepipatella spp.[a]
Concholepas concholepas[b]
Chiton spp.
Balanus spp.

Rocky Subtidal Zone

Aulacmoya ater
Thais (*Stramonita*) *chocolata*
Thais (*Stramonita*) *haemastoma*[c]
Thais sp.

Sandy Intertidal Zone/Upper Subtidal Zone

Donax (*Chion*) *obesulus*
Mulinia edulis

Sandy Subtidal Zone

Choromytilus chorus
Eurhomalea rufa
Protothaca (*Protothaca*) *thaca*
Mesodesma donacium
Polinices (*Polinices*) *uber*
Oliva (*Oliva*) *peruviana*

Sandy/Muddy Bay Floor

Argopecten purpuratus

Other

Scutalus spp.—lomas (land)
Petricola denticulata—in polychaete worm (false coral, "piedra pomez") blocks in the upper subtidal zone

conditions similar to those that now obtain in the area. The following paragraphs discuss exceptions and limitations to this observation.

All of the taxa found at Lo Demás are indigenous to the cool waters of the Peruvian Molluscan Province except *Spondylus* (Table 29; Marincovich, 1973; Olsson, 1961; Rodríguez H., 1984; Sandweiss, 1982). *Spondylus* is a red and white bivalve covered with spiny projections; although native to the warm waters of Ecuador, Colombia, and Central America,[79] it became an important ritual item in the prehistoric Central Andes. First appearing in Peruvian sites in the Late Preceramic Period (Feldman, 1980), *Spondylus* had spread throughout the Central Andes by the Early Horizon (Paulsen, 1974). During late pre-Hispanic times, trade in this shell became extremely important (Murra, 1975). Rostworowski (1970:152–153, 161) believes that acquisition of *Spondylus* was a major objective of the Chincha merchants who

Table 29.—*Ranges of marine mollusk taxa from Lo Demás (compiled from Coan, 1983; Lorenzen et al., 1979; Olsson, 1961; Marincovich, 1973; and Peña G., 1970).* [a] *Although reported distributions of this species (and other species of this genus) do not extend south of Chiclayo, Peru,* Polinices uber *has been identified in a number of sites from central Peru (e.g., Garagay, in Lima, Sandweiss, 1982). The discrepancy may be due to a misidentification, a shift in range, or incomplete collections of modern specimens. As a rare item (two occurrences) in the mollusk sample from Lo Demás, the uncertainties related to* P. uber *do not cause a significant problem in interpretation.*

Taxon	Range
Semimytilus algosus	Paita, Peru, to Arauco, Chile
Choromytilus chorus	Pacasmayo, Peru, to Tierra del Fuego
Aulacomya ater	Callao, Peru, to Straits of Magellan
Perumytilus purpuratus	Ecuador to Straits of Magellan
Spondylus spp.	Warm waters from Ecuador north
Argopecten purpuratus	Paita, Peru, to Coquimbo, Chile
Eurhomalea rufa	North Peru to Concepción, Chile
Protothaca (*Protothaca*) *thaca*	Callao, Peru, to Chonos Archipelago
Petricola (*Petricola*) *denticulata*	Lobos Island, Peru, to Chonos Archipelago
Mulinia edulis	Callao, Peru, to Straits of Magellan
Mesodesma donacium	Sechura, Peru, to Valparaiso, Chile
Donax (*Chion*) *obesulus*	Manabí, Ecuador, to Bahía Moreno, Chile
Fissurella spp.	Cold waters of Peru and Chile
Acmaea spp.	Cold waters of Peru and Chile
Tegula (*Chlorostoma*) *atra*	Pacasmayo, Peru, to Straits of Magellan
Prisogaster niger	Pacasmayo, Peru, to Straits of Magellan
Calyptraea (*Trochita*) *trochiformis*	Manta, Ecuador, to Valparaiso, Chile
Crepipatella spp.	Cold waters of Peru and Chile
Polinices (*Polinices*) *uber*	Baja California to north Peru[a]
Thais (*Stramonita*) *chocolata*	Paita, Peru, to Valparaiso, Chile
Thais (*Stramonita*) *haemastoma*	Baja California to Valparaiso, Chile
Concholepas concholepas	Callao, Peru, to Straits of Magellan
Oliva (*Oliva*) *peruviana*	Galapagos Islands to Valparaiso, Chile
Chiton spp.	Cold waters of Peru

sailed north to trade in Ecuador (*see* Chapter 2). However, we found only three fragments of *Spondylus* in Lo Demás:[80] two are bits of spine and one is a finished circular bead (*see* Chapter 8).

The geographic range of the Peruvian Province[81] mollusks found at Lo Demás includes the Chincha valley. However, from 1983 to 1986, Rodríguez and I saw live specimens of only four of these species in Chincha: *Donax obesulus, Semimytilus algosus, Thais chocolata,* and *Prisogaster niger. Donax* and *Semimytilus* are the most abundant shells at Lo Demás. We also found empty *Mulinia edulis* valves along the beach. The 1982–1983 El Niño affected the distribution of many mollusks, displacing species such as *Mesodesma donacium* hundreds of kilometers to the south of their usual range (Arntz, 1986; Rollins et al., 1986); the four species observed live in recent years in Chincha are among those most resistant to the effects of El Niño (Arntz, 1986; DeVries, 1987; Rollins et al., 1990).

El Niño could account for the absence of many species in the Chincha area in recent years;[82] the modern Chincha shoreline includes the appropriate habitats for the taxa listed in note 82, and the possibility exists that the inhabitants of Lo Demás collected these mollusks locally. However, the remaining Peruvian Molluscan Province species found at Lo Demás probably came from some area other than the immediate Chincha shoreline.[83] Many of these mollusks are rock-dwellers which live in the upper intertidal (splash) zone (*Perumytilus purpuratus*),[84] the intertidal zone of rocky promontories (*Acmaea* spp., *Concholepas concholepas, Fissurella* spp.), or subtidal rocky bottoms (*Aulacomya ater*). The entire length of the Chincha shoreline (ca. 40 km from the Quebrada Topará south to the edge of the Pisco valley) is sandy beach; the only rocks that we observed are small boulders in the lower intertidal zone near the mouth of the Río Chico (*see* Fig. 1). Local fishermen state that there are no large, submerged rocky areas off the Chincha coast; this anecdotal information is consistent with the absence of bedrock outcrops along or near the Chincha shore and with the absence of subtidal rock-dwelling mollusk valves in the beach deposits. The closest known sources for the rock-dwellers listed above are the Paracas Peninsula, 35 to 40 km to the south of Lo Demás, and the Chincha Islands, a similar distance to the southwest. The one recovered specimen of *Argopecten purpuratus* (scallop) almost certainly came from the Paracas area. This scallop lives on bay floors; the nearest bay is San Andrés, on the north side of the Paracas peninsula.

Choromytilus chorus is the final species with a problematic provenience. Since Late Preceramic times, the northern limit of *Choromytilus* has apparently shifted south from somewhere between the Moche and Lambayeque valleys to the central coast between Paracas and Ancón. Within the latter area, reports of live populations are geographically sporadic. Valdiviezo (personal communication) observed small populations of *Choromytilus* in the late 1970s at Santa Rosa, near Ancón on the northern side of Lima. Early in this century, Murphy (1921: 50) noted abundant beds of this species from sand banks at the Bahía de Independencia on the south side of the Paracas peninsula, and in 1983, Carlos Elera (personal communication, 1983) collected live specimens from nearby Laguna Grande. *Choromytilus chorus* lives in banks in sandy and muddy bottoms with scattered rocks, with an apparent preference for protected areas such as bays. Although it might have inhabited the Chincha area in the past, the open shoreline there today does not seem favorable for *Choromytilus.*

These data suggest that the late pre-Hispanic inhabitants of Lo Demás got *Choromytilus chorus* from the Paracas area. Trade or exchange for this species is an old tradition in the Andes. Importation of *Choromytilus* into the highlands for nonsubsistence purposes began at least as early as the Early Archaic Period and continued throughout prehistoric time. On the coast, the purple mussel had both subsistence and nonsubsistence functions, the latter as paint containers and/or as painted shells used for decoration or other ritual activities (Sandweiss, 1982: 224, 1985*a*). Trade in *Choromytilus* valves along the littoral may have brought shells of this species to areas where it no longer lived. At Lo Demás, *Choromytilus* remains include a number of specimens with pigment (*see* Chapter 8, section on Bone and Shell Objects, for a description).

Primary midden context, occasional charring, and the rarity of intentional modification of the mollusk valves from Lo Demás suggest that the inhabitants of the site used shellfish mainly as a source of food (Table 26). However, some imported species had intentional nonsubsistence uses (*Spondylus* and *Choromytilus—see above*), while specimens of several local species entered the site accidentally. This latter category includes the barnacles (*Balanus* spp.), the *Petricola denticulata,* many of the *Prisogaster* *niger,* and some of the *Semimytilus algosus* and *Tegula atra* specimens. Peruvian coastdwellers do not eat barnacles today, and their ancestors probably did not do so, either. We found few barnacles in Lo Demás, mostly small; several specimens were attached to valves of other species such as *Semimytilus algosus.* The few examples of *Petricola denticulata* found in Lo Demás probably arrived with the calcareous worm heads in which it lives (*see* note 82). Among the abundant remains of *Semimytilus algosus* were a few closed, articulated valves. Many of the *Prisogaster niger* snails still had their opercula, and we found a number of loose opercula of this species. One of the few intact *Tegula atra* valves also had its operculum in place. Closed, articulated bivalves and operculum-sealed gastropods could not have been eaten.

Prisogaster and *Tegula* both live in the same habitat as *Semimytilus.* A common method of collecting *Semimytilus* involves scraping large quantities of this small mussel off of the rocks on which it lives; such a procedure results in the accidental collection of very small *Semimytilus* valves along with *Prisogaster* and *Tegula.* The articulated specimens of these species found in Lo Demás were probably collected in this way.

Quantitative Analysis

Objectives and limitations. —The quantitative analysis of molluscan remains can have two major functions: to estimate the dietary contribution of the mollusks and to recognize changing or contrasting patterns of mollusk use.

Dietary reconstruction involves estimating the weight of the meat originally contained in the mollusk valves found in an archaeological assemblage. Attempts to make such calculations have a long history (*see* Koloseike, 1969, for a review of early efforts; *see* Rollins et al., 1990, for more recent studies); the last two decades have seen the development of fairly accurate techniques for meat weight estimation based on allometric models and regression analysis (Parmelee and Klippel, 1974; Reitz et al., 1987; Sandweiss, 1979, 1985*b*). Although regression estimates of live weights from skeletal elements of vertebrate animals continue to be problematic (Grayson, 1984:172–174), the low number of skeletal elements in mollusks (maximum of two) and the direct morphological relationship between shell (container) and meat (contained) make mollusks more successful targets than vertebrates for meat weight analysis.[85] Comparison of experimental results for various Peruvian mollusks (Sandweiss, 1979, 1985*b*; Tomka, 1980) indicates that regression coefficients are species-specific, though Reitz et al. (1987) found that regressions on Florida mollusk data pooled by genus provided acceptable estimates. These observations present an empirical limitation on meat weight estimation—experimental data must be available for each species or at least genus for which meat weight needs to be estimated. I have run experiments on five Peruvian taxa: *Donax obesulus* (Sandweiss, 1979), *Semimytilus algosus, Perumytilus purpuratus, Mesodesma donacium,* and *Crepipatella* spp. (Sandweiss, 1985*b*); Tomka (1980) provides data for *Aulacomya ater.* These six species account for 89.1% by weight and 87.9% by MNI of the Lo Demás sample (Table 27). Nevertheless, the results of the meat weight analyses are not presented here because of a further limitation on the use of such data; interpretation of the importance of shellfish in prehistoric diet requires equivalent quantitative estimates of the food value provided by all other food types found in the site under analysis. Estimation of vertebrate meat weight from archaeological remains is problematic (and no one has yet published experimental data for Peruvian fish or terrestrial animals), while the dietary contribution of botanical remains is even harder to quantify.

Recognition of changing patterns of mollusk use requires calculating the relative frequencies of different species through time in a stratified archaeological deposit. Identifying, weighing, and counting the sample is straightforward; problems arise at the interpretive stage because of the difficulty in assessing the contributions of cultural preference[86] and natural availability in forming the midden (*see* Rollins et al., 1990:470–471). The difference is crucial; changes resulting from cultural preference provide information on human behavior, while those resulting from natural availability indicate environmental alterations.[87] The two kinds of processes must be distinguished in order to draw meaningful conclusions from the molluscan data. In this study, I have used the following assumption to differentiate some of the changes due to preference from some of those resulting from availability: *changes in frequency of species in a stratigraphic sequence reflect changes in availability*[88] *rather than preference when all of the involved species remain well represented in the contrasting archaeological levels.* The few ethnographic studies of shellfish collectors (e.g., Bigalke

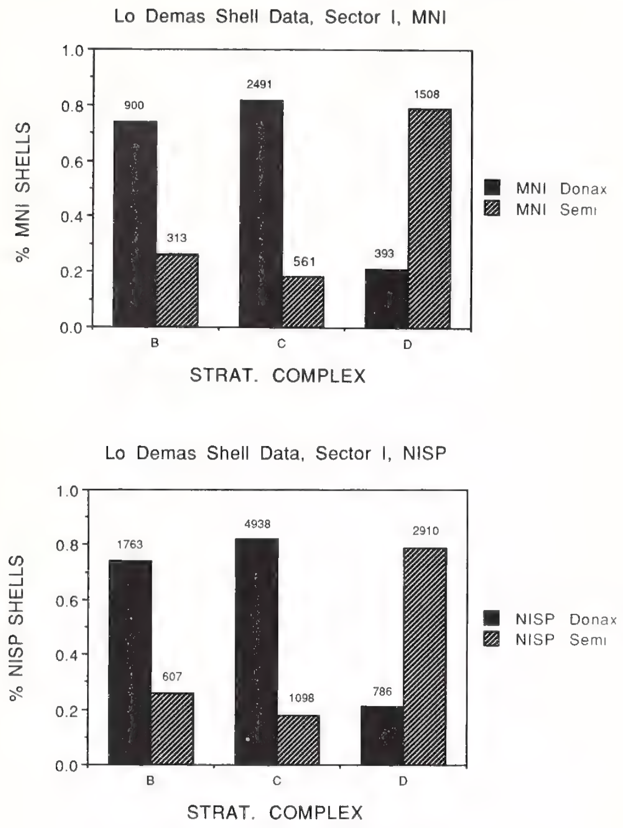

Fig. 54.—Relative abundance of the mollusks *Donax obesulus* and *Semimytilus algosus* in the molluscan sample from Stratigraphic Complexes B, C, and D in Sector I of Lo Demás, by MNI and by NISP. Histograms show percent of *Donax* and *Semimytilus* in each level; in calculating the percentages, only these two species were used. The numbers above the histograms show the absolute abundance of each species in each complex.

and Voight, 1973; Meehan, 1977, 1982) do not support relative shifts of preference—a species either is eaten or it is not. The disappearance or appearance of a species in an archaeological sequence may result from either natural or cultural causes, though my personal observations in Peru suggest that a preference hierarchy imposed on natural availability accounts for most changes of this sort (*see* Sandweiss, 1989:390, footnote 216).

The above assumption does not apply to contrasting frequencies between different parts of a site when the exact contemporaneity of the strata in each part of the site cannot be established. Interpretations based on such contrasts are more general and less secure than those drawn from changes within a single stratigraphic sequence. Even when contemporaneity of strata is clear, different functional contexts of different parts of a site[89] introduce new possibilities for cultural explanations of contrasting frequencies. Comparison of the molluscan assemblages from Sector I (common residences) and Sector IV (elite structures) of Lo Demás provides a case in point (*see below*).

Analysis by stratigraphic complex in Sector I.—For this analysis, the different members of each stratigraphic complex in Sector I were pooled into complex totals, in order to see changes through time in predominant molluscan taxa (Sandweiss, 1989: Tables 33–36). One major change takes place in the stratigraphic sequence in Sector I: in Complex D (the most recent deposit), *Semimytilus algosus* replaces *Donax obesulus* as the dominant species in terms of both weight and MNI (Table 30, Fig. 54). *Donax* had dominated the molluscan remains in all three earlier complexes (A to C). In Complex D, an increase in *Prisogaster niger* accompanied the increase in *Semimytilus algosus.* Many of the *Prisogaster* specimens are quite small and still have their opercula; they were probably collected accidentally with the *Semimytilus,* as both species share the same rocky intertidal habitat.

Statistically, the differences in the frequency of *Donax* and *Semimytilus* between Complexes B and C and between Complexes C and D cannot be due to random variation in samples drawn from the same parent population (*see* Table 31); the *Donax/Semimytilus* reversal between Complexes C and D reflects a real change (whatever the cause). This result holds true for the shells when compared by weight, NISP (Number of Identified Specimens), and MNI aggregated by provenience or by complex.[90]

We first noticed the *Donax/Semimytilus* reversal while analyzing the 1983 remains (Complexes A, C, and D) (Rodríguez H., 1984; Sandweiss, 1988). The samples from the 1984 excavations (Subunits 3B and 10D) show the same pattern; Complex B (not present in the 1983 excavation) fits the pattern, with a high proportion of *Donax.* This correspondence confirms the correlation of the stratigraphic complexes in the 1983 and 1984 excavation areas of Sector I based on strata orientation and architectural associations (*see* Chapter 5). Analysis of the mollusks by provenience within each complex corroborates the grouping of the strata into complexes; the predominance of *Semimytilus* begins immediately above the lowest provenience of Complex D, while *Donax* predominates in virtually all proveniences of Complexes A to C.[91]

Following the assumption discussed above concerning changes in species frequencies, the *Donax/*

Table 30.—Donax peruvianus *versus* Semimytilus algosus, *Lo Demás Sector I, Stratigraphic Complexes A to D, by weight and by MNI. Counts are absolute, percentages are relative to all molluscan remains from each stratigraphic complex. Compare to Fig. 54, which plots* Donax *against* Semimytilus *for Complexes B to D.*

	A		B		C		D	
	Wgt	%	Wgt	%	Wgt	%	Wgt	%
D. obesulus	44.9	77.8	1,244.7	74.1	3,360.0	72.1	606.1	17.8
S. algosus	2.5	4.3	269.3	16.0	914.8	19.6	2,190.2	64.1

	A		B		C		D	
	MNI	%	MNI	%	MNI	%	MNI	%
D. obesulus	38	71.7	947	63.9	2,616	72.2	472	16.9
S. algosus	6	11.3	359	24.2	633	17.5	1,549	55.4

Semimytilus reversal represents a change in the availability of these mollusks; both species are well represented in all complexes, despite the real reversal in dominance. Possible explanations for the increased relative abundance of *Semimytilus* fit into three categories:

1) Overexploitation of *Donax* by local collectors, leading to decreased availability of this species. The continued, substantial presence of *Donax* in Complex D without a noticeable decrease in size argues against overexploitation.

2) Climate change affecting *Donax* more than *Semimytilus.* Because *Donax* and *Semimytilus* are both indigenous to the same cool water conditions and because both are present in Chincha today, any climate change during the Late Horizon occupation of Lo Demás would necessarily have been minor and/or temporary. Under these conditions, El Niño provides the only likely possibility for a short term change in coastal climate. El Niño does affect different mollusk species to different degrees (Arntz, 1986; Rollins et al., 1986). However, in Chincha as well as elsewhere on the coast, both *Donax* and *Semimytilus* recovered from the major 1982–1983 El Niño in a few months (Arntz, 1986; Rollins et al., 1990; personal observations).

3) Changes in the physical environment leading to increased rocky intertidal area or decreased sandy intertidal area in the vicinity of Lo Demás. Several natural processes could have produced such changes: the Río Chico (Fig. 1) might have brought more rocks to its mouth; the river could have shifted its mouth to the north, closer to Lo Demás (today, intertidal rocks and *Semimytilus* occur in Chincha only at the river mouths); or shoreline erosion could have removed sand from the beach and exposed previously buried rocks, which subsequently would have been reburied by the coastal progradation mentioned by historical sources (e.g., Cánepa P., 1982:88; Coker, 1908–VI:89; Pachas T., 1983:40; *see* Chapter 5).

Within the third category, there is an intriguing possibility that the molluscan evidence reflects the construction of a jetty or pier near Lo Demás. The documentary sources concerning Chincha mention the valley's importance as a maritime trading power (*see* Chapter 2). Pedro Pizarro wrote that the Inka Atawalpa told him in Cajamarca of the Inka's great friend the lord of Chincha, who had "100,000 balsas [trading rafts] on the sea" (Pizarro, 1965 [1571]: 232). Although certainly an exaggeration, the large figure cited by Pizarro demonstrates the importance of the trading rafts to Chincha—they are the symbol by which the Inka identified the lord of Chincha. Lo Demás lies directly between the shore and La Centinela, the Chincha capital and Inka administrative center (Menzel and Rowe, 1966), so a port facility built to service the lord of Chincha's trading ventures would have been close to Lo Demás. Though I saw no traces of such a facility, the rapid progradation of the shoreline would have buried the rocks of a low-lying jetty. Geophysical prospecting

Table 31.—*Statistical analysis of the variation in frequency of* Donax obesulus *relative to* Semimytilus algosus *between stratigraphic complexes in Sector I, Lo Demás. Analyses were run on the data for NISP, MNI aggregated by stratigraphic complex (SC), MNI aggregated by provenience (pr.), and weight. Results are reported as the observed difference in the percentage of* Donax *between two levels expressed as standard deviations from the expected difference (0) based on the null hypothesis that each pair of complexes was drawn from the same parent population.*

Between Complexes	Number of Standard Deviations			
	NISP	MNI (SC)	MNI (pr.)	Weight
C and D	58.67	42.38	42.13	58.87
B and C	7.60	5.42	5.84	9.47

Table 32.—*Total weight and MNI (Minimum Number of Individuals) of mollusks by taxon for Sector I, Lo Demás. MNI was aggregated by provenience. An asterisk indicates less than 0.1%. A dash means not applicable. Numbers in parentheses following MNI indicate the number of levels with fragments of a taxon but no MNI indicator; each of these levels contributed one count to the listed MNI. Data from Sandweiss (1989:Tables 33–36).*

Genus/Species	Weight	%	Rank	MNI	%	Rank
Semimytilus algosus	3,376.8	34.4	2	2,547 (26)	32.0	2
Choromytilus chorus	29.5	0.3	12	30 (29)	0.4	9
Aulacomya ater	265.0	2.7	3	91 (59)	1.1	7
Perumytilus purpuratus	2.1	*	19	8 (5)	0.1	13
Spondylus spp.	0.1	*	24	1 (1)	*	19
Argopecten purpuratus	4.7	*	16	1 (1)	*	19
Protothaca thaca	219.4	2.2	4	109 (60)	1.4	6
Petricola denticulata	1.7	*	21	4 (3)	0.1	17
Mulinia edulis	50.1	0.5	9	158 (31)	2.0	5
Mesodesma donacium	82.5	0.8	8	194 (14)	2.4	4
Donax obesulus	5,255.7	53.6	1	4,073 (12)	51.1	1
Fissurella spp.	17.1	0.2	13	11 (5)	0.1	12
Acmaea spp.	0.1	*	24	1	*	19
Tegula atra	16.5	0.2	14	22 (2)	0.3	10
Prisogaster niger	183.9	1.9	5	616 (5)	7.7	3
Calyptraea trochiformis	0.1	*	24	1	*	19
Crepipatella spp.	5.9	0.1	15	16 (2)	0.2	11
Polinices uber	2.0	*	20	1	*	19
Thais chocolata	108.8	1.1	6	60 (40)	0.8	8
Thais sp.	2.5	*	18	3 (2)	*	18
Concholepas concholepas	36.4	0.4	11	5 (4)	0.1	15
Unidentified pelecypod	4.7	*	16	1	*	19
Scutalus spp.	0.7	*	22	8	0.1	13
Chiton spp.	0.3	*	23	5 (5)	0.1	15
Balanus spp.	38.6	0.4	10	—	—	—
Unidentified	107.0	1.1	7	—	—	—
Total	9,812.2			7,966		

could probably detect this kind of feature. Historical records for the earlier part of this century provide a rationale for the construction of a jetty in Chincha; landing a boat on the open Chincha shore is extremely difficult (e.g., Coker, 1908–VI:89). Small totora fishing craft can land without too much problem, but keeled, European craft as well as heavily laden cargo rafts require some sort of port facility. That such a facility should have been constructed during the Late Horizon and not earlier is consistent with the hypothesis that Chincha's maritime trading activities were significantly expanded under Inka rule (*see* Chapter 2).

Analysis by sector.—The samples from Sectors I and IV are remarkably similar in terms of the taxa present and the proportional representation of each taxon (Tables 32 and 33). The only notable difference is in the percent by weight of three of the largest species present: *Aulacomya ater, Thais chocolata,* and *Concholepas concholepas.* In each case, the Sector IV sample has a slightly higher proportion of these species than does the total Sector I sample (the percentage of total weight for the three species combined is 15.0% in Sector IV and 4.2% in Sector I). However, the proportions for MNI do not show the same trend; they are almost identical for all three species in both samples (the percentage of total MNI for the three species combined is 2.2% in Sector IV and 2.0% in Sector I). These data indicate that the individuals of the three species were larger in Sector IV than in Sector I. Although conclusions drawn from the comparison of the two samples must remain very tentative until a larger sample becomes available (esp. from Sector IV), the greater representation of the large species in the Sector IV sample suggests that the inhabitants of that sector had selective or differential access to molluscan resources. Such privilege fits the data for other classes of remains as well as the architectural evidence for the elite nature of Sector IV. Of course, this hypothesis assumes that larger specimens of the large species held greater value for the late pre-Hispanic inhabitants of Chincha than did the smaller specimens.

Another important factor is the local/imported

Table 33.—*Total weight and MNI (Minimum Number of Individuals) of mollusks by taxon for Subunit 26D, Sector IV, Lo Demás. MNI was aggregated by provenience. An asterisk indicates less than 0.1%. A dash means not applicable. Numbers in parentheses following MNI indicate the number of levels with fragments of a taxon but no MNI indicator; each of these levels contributed one count to the listed MNI.*

Genus/Species	Weight	%	Rank	MNI	%	Rank
Semimytilus algosus	2,031.0	29.5	2	2,328 (4)	40.1	2
Choromytilus chorus	10.3	0.1	13	16 (15)	0.3	11
Aulacomya ater	299.1	4.3	4	58 (19)	1.0	7
Permytilus purpuratus	15.7	0.2	12	35 (12)	0.6	10
Spondylus spp.	0.1	*	23	2 (2)	*	15
Eurhomalea rufa	1.6	*	16	1	*	18
Protothaca thaca	46.3	0.7	9	36 (21)	0.6	9
Mulinia edulis	23.3	0.3	11	68 (12)	1.2	6
Mesodesma donacium	55.1	0.8	7	157 (14)	2.8	4
Donax obesulus	3,485.5	50.6	1	2,557 (1)	45.1	1
Fissurella spp.	0.2	*	21	2 (2)	*	15
Acmaea spp.	0.1	*	23	1	*	18
Tegula atra	8.8	0.1	14	79 (3)	1.4	5
Prisogaster niger	51.4	0.7	8	240 (2)	4.2	3
Crepipatella spp.	2.0	*	15	10 (2)	0.2	12
Polinices uber	0.6	*	19	1	*	18
Thais chocolata	612.3	8.9	3	54 (28)	1.0	8
Thais sp.	1.5	*	17	1	*	18
Concholepas concholepas	126.6	1.8	5	12 (10)	0.2	13
Oliva peruviana	0.8	*	18	1	*	18
Scutalus spp.	0.4	*	20	9 (2)	0.2	14
Chiton spp.	0.2	*	21	2 (2)	*	15
Balanus spp.	45.8	0.7	10	—	—	—
Unidentified	64.5	0.9	6	—	—	—
Total	6,883.2			5,670		

criterion; two of the three large species with greater representation in Sector IV were probably imported from neighboring valleys or islands (*see above*). Comparing the samples from the two sectors in terms of the proportion of marine taxa most likely to have come from outside the Chincha valley,[92] the Sector IV sample has about twice as much imported shell as Sector I by weight (6.6% in Sector IV vs. 3.6% in Sector I), though only about 20 percent more by MNI (2.3% vs. 1.9%, Table 34). The observed difference by weight between the frequency of imported shells in Sectors I and IV is 8.75 standard deviations from the frequency expected if there were no real difference between the two samples ($P < 0.0001$). This result confirms that the difference is statistically real. The observed difference by MNI is only 1.31 standard deviations from the expected difference under the null hypothesis of no difference in the parent populations ($P > 0.19$). The greater difference in weight than in MNI reflects the larger size of individual specimens in Sector IV; thus, the data on importation of shells support the hypothesis that the Sector IV inhabitants enjoyed differential access to shellfish. However, the privilege of selectivity apparently applied only to food species; both sectors have equivalent—and minimal—representation of the two primary nonsubsistence taxa, *Choromytilus* and *Spondylus*.[93]

A final point of comparison between the shell samples from Sectors I and IV concerns the relative predominance of *Semimytilus* and *Donax*. The radiocarbon dates (Chapters 5 and 11), the ceramics (Chapter 7), and the figurines (Chapter 8) indicate that Sector I and Sector IV are broadly contempo-

Table 34.—*Percentage of imported shell by weight and MNI (aggregated by provenience) in the samples from Sectors I and IV, Lo Demás* (see *note 92 for a list of shells considered as imported).*

	Weight	MNI
I (% of total shells)	3.6%	1.9%
IV (% of total shells)	6.6%	2.3%
Ratio IV/I (%)	1.833	1.211
Difference in frequencies between Sectors I and IV expressed as standard deviations from the expected difference (0) under the null hypothesis of no difference in parent populations	8.75	1.31

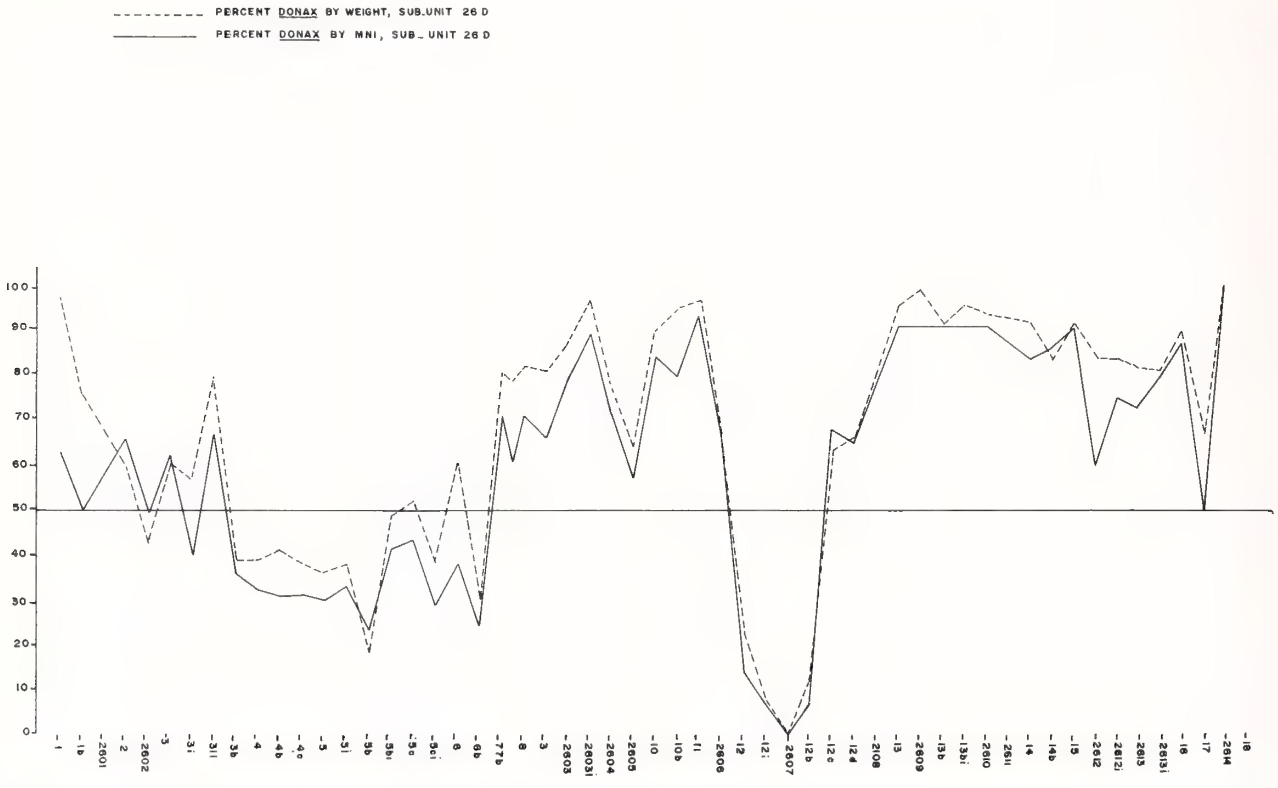

Fig. 55.—Percent of the mollusk *Donax obesulus* relative to *Semimytilus algosus* by level in Lo Demás, Sector IV, Subunit 26D, for MNI (solid line) and shell weight (dashed line).

raneous. Therefore, I would expect that the two species which vary so notably in predominance in the Sector I sequence would have a similar pattern in Sector IV. Such a pattern would allow more exact cross-dating of the two parts of the site. In fact, the Sector IV sample shows several shifts (Fig. 55, *see* Fig. 10 for Subunit 26D statigraphy). Unlike Sector I, *Donax* predominates in the upper proveniences (1 to 3) and *Semimytilus* predominates in the next lowest group of strata (3b to 6b). Below these two groups, however, *Donax* (7 to 11, 12c to 17) alternates with *Semimytilus* (12 to Feature 2607). Several alternative hypotheses could explain this pattern.

1) The Subunit 26D strata do not overlap in time with the Sector I occupation. This hypothesis can be rejected in light of the other data on chronology.

2) The Subunit 26D mollusks do not reflect local availability in the same way as the Sector I remains, perhaps due to access privileges. In this case, there should not be any major shifts in predominant species. The existence of clearly marked species shifts thus serves to reject this hypothesis.

3) The Subunit 26D deposit covers an overlapping but greater length of time than the Sector I strata. Considering the independent chronological data indicating broad contemporaneity between the two deposits, this alternative is the most strongly supported. In this case, the problem becomes one of determining which Sector IV *Semimytilus*/*Donax* dyad corresponds to the Sector I complexes. The upper proveniences of Subunit 26D probably either postdate the Sector I deposit or consist of mixed material. As an elite area, occupation of Sector IV may well have continued further into the postconquest period (with its radical population decline) than did Sector I. However, we found no European artifacts in Sector IV, though some of the animal feces in the upper proveniences looked very much like sheep/goat (*see below*). The rather early radiocarbon date (out of stratigraphic order) argues for the possibility of mixing; in this case, the predominance of *Donax* could represent earlier conditions.

Following this line of reasoning, the group of proveniences (3b to 6b) with *Semimytilus* predominance would be equivalent to Complex D in Sector I. Proveniences 7 to 11 would correspond to Complexes C and B, leaving two possible explanations for proveniences 12 to 12b and 12c to 17. These lower sets may pre-date the Sector I deposits or the small block of *Semimytilus*-dominated proveniences (12 to 12b) may represent a statistical anomaly. In the latter case, Complexes C and B of Sector I match proveniences 7 to 17 in Subunit 26D. I prefer the second possibility for several reasons. The use of Inka-related rectangular *adobes* indicates that the walls built at about the time when provenience 17 was deposited postdate the Inka conquest of the valley (*see* Chapters 4 and 6); the Cuzco Polychrome A sherd from Complex B in Sector I (*see* Chapter 7) demonstrates that the Sector I deposit also postdates the Inka conquest of Chincha. Contemporaneity is also shown by the radiocarbon dates; the date from the lower deposits in Subunit 26D corresponds nicely to those for Sector I. The assignment of both sectors to the Late Horizon based on the artifacts leaves little time for the deposition of Complexes B to D in Sector I and proveniences 17 to 1 in Sector IV. Both the renewed construction activity in Sector IV and the initial occupation of Sector I may well reflect the changes accompanying the incorporation of Chincha into the Inka empire.

FISH REMAINS

Like mollusks, fish remains have great potential for archaeological interpretation (e.g., Casteel, 1976). The fish bones recovered at Lo Demás provide information on the general marine environment, on fishing and fish-processing practices, and on differential access to resources by elite and nonelite residents of the site. The fish bones, like the shells, also help confirm the validity of the stratigraphic complexes in Sector I originally defined by strata orientations and architectural associations (*see* Chapter 5).

The fish remains come from the same primary midden contexts as the shell remains. The studied sample includes all of the fish bones recovered in the ¼″ screen from the 1983 test excavations (Sector I), from Subunits 3B and 10D (Sector I), and from Subunit 26D (Sector IV). Subunit 26D was treated as a single stratigraphic complex; the subdivisions suggested by the shell remains (*see above*) were tested against the fish remains with ambiguous results.

Gilber Mariano A. (Javier Prado Natural History Museum, Lima, Peru) identified the fish bones from Lo Demás (Mariano A., 1984, 1985, 1986), classifying specimens of ten taxa to the species or genus level. These taxa are distributed among six families; specimens from two other families could not be identified at a lower taxonomic level (Table 35). Of a total of 7,706 analyzed specimens, 5,896 (76.5%) pertain to the ten identified genera or species.

Table 35.—*Taxonomic list of identified fish species from archaeological contexts at Lo Demás (from Mariano A., 1984, 1985, 1986). Orders and families are listed without specific representatives when no specimens were identified more precisely than the order or family level.*

- SQUALIFORMES
- CLUPEIFORMES
  - Clupeidae
    - *Brevoortia maculata*
    - *Sardinops sagax*
  - Engraulidae
    - *Engraulis ringens*
    - *Anchoa nasus*
- SILURIFORMES
  - Ariidae
- PERCIFORMES
  - Haemulidae
    - *Anisotremus* sp.
  - Sciaenidae
    - *Cynoscion analis*
    - *Paralonchurus peruanus*
    - *Sciaena* sp.
  - Mugiloididae
    - *Mugiloides* sp.
  - Scombridae
    - *Sarda sarda chiliensis*
  - Centralophidae

Methodology

The laboratory analysis of the fish remains from Lo Demás involved several phases. The first phase was the preparation of a comparative collection. Mariano (1984) began by determining the species of fish now indigenous to the Chincha area and therefore most likely to have been available to late pre-Hispanic Chincha fishermen. To make this list, Mariano consulted Velez's (1975) tables of common species from each marine habitat of the nearby Pisco area. Observations and published descriptions of the Chincha coast indicate that available habitats today include or may include the following zones: coastal pelagic, sandy to muddy benthic, and sandy to rocky benthic. Available indicators of marine conditions during the Late Horizon occupation of Lo Demás suggest that a similar set of habitats characterized the Chincha coast at that time. Cross-tabulating these habitats with Velez's tables produced a list of the 30 most common fish species for Chincha (*see* Table 36). Fresh specimens of each of these species were then collected, using Chirichigno's (1974) key for

Table 36.—*Taxonomic list of the 30 most common fish species in the Pisco area from the coastal pelagic, sandy to muddy benthic, and sandy to rocky benthic habitats (list compiled by Mariano A. [1984] from Velez [1975]). Compare this list with the taxa actually identified at Lo Demás (Table 35). Not included in this list are the order Squaliformes, of the superorder Euselachii and the class Chondrichthyes; this order, which consists of the sharks, did not form part of our comparative sample. However, shark vertebrae are quite distinctive, and Mariano identified several specimens in the Lo Demás sample (thus, "Squaliformes" appears in Table 35).*

- Class: CHONDRICHTHYES
    - Superorder: SELACHOIDEA
    - Order: AMNIFORMES
        - Family: Triakidae
            - *Mustelus mento* ("tollo blanco")
    - Superorder: HIPOTREMATA
    - Order: RAJIFORMES
        - Family: Rhinobatidae
            - *Rhinobatus planiceps* ("guitarra")
        - Family: Rajidae
            - *Psammobatis brevicaudatus* ("pastelillo")
        - Family: Urolophidae
            - *Urotrygon peruanus* ("castelillo")
        - Family: Myliobatidae
            - *Myliobatis peruvianus* ("raya de punta")
- Class: HOLOCEPHALI
    - Order: CHIMAERIFORMES
        - Family: Callorhindhidae
            - *Callorhynchus callorhinchus* ("peje gallo")
- Class: OSTEICHTHYES
    - Subclass: ACTINOPTERYGII
    - Infraclass: TELEOSTOMA
    - Division I
        - Superorder: CLUPEOMORPHA
        - Order: CLUPEIFORMES
            - Family: Clupeidae
                - *Brevoortia maculata* ("machete")
                - *Sardinops sagax* ("sardina")
            - Family: Engraulidae
                - *Engraulis ringens* ("anchoveta")
                - *Anchoa nasus* ("anchoveta blanca")
    - Division III
        - Superorder: SILURIMORPHA
        - Order: SILURIFORMES
            - Family: Ariidae
                - *Arius peruvianus* ("bagre")
        - Superorder: PARACANTHOPTERYGII
        - Order: BATRACHOIDIFORMES
            - Family: Batrachoididae
                - *Aphos porosus* ("pez fraile")
        - Order: GADIFORMES
            - Family: Gadidae
                - *Merlucius gayi peruanus* ("merluza")
        - Superorder: ATHERINIFORMES
        - Order: ATHERINIFORMES
            - Family: Atherinidae
                - *Odonthesthes regia regia* ("pejerrey")
        - Order: PERCIFORMES
            - Family: Malacanthidae
                - *Caulolatilus princeps* ("peje blanco")
            - Family: Carangidae
                - *Trachurus symmetricus* ("jurel")
            - Family: Haemulidae
                - *Anisotremus scapularis* ("chita")
                - *Isacia conceptionis* ("cabinza")
            - Family: Sciaenidae
                - *Cynoscion analis* ("ayanque," "cachema")
                - *Menticirrus ophicephalus* ("mis mis," "bobo")
                - *Stellifer minor* ("mojarilla")
                - *Paralonchurus peruanus* ("coco")
                - *Sciaena gilberti* ("lorna")
            - Family: Mugilidae
                - *Mugil cephalus* ("lisa")
            - Family: Mugiloididae
                - *Mugiloides chiliensis* ("bacalao," "camote")
            - Family: Scombridae
                - *Sarda sarda chiliensis* ("bonito")
                - *Scomber japonicus peruanus* ("caballa")
            - Family: Centralophidae
                - *Seriolella violacea* ("cojinoba")
        - Order: PLEURONECTIFORMES
            - Family: Bothidae
                - *Etropus ectenes* ("lenguado")
        - Order: TETRAODONTIFORMES
            - Family: Tetraodontidae
                - *Sphoeroides annulatus* ("pez globo," "tamborín")

identification. After removing the flesh and cleaning the bones, Mariano classified each of the skeletal elements according to species and type of bone.

The second phase of research was identification of fish bones from Lo Demás (Mariano, 1984, 1985, 1986). Using the comparative collection and published references, the remains from each provenience were first sorted by skeletal element; each bone was then identified to the lowest possible taxonomic level (order, family, genus, or species). Bones with no relationship to any of the available comparative material were listed by size of the fish (small or large fish).

The MNI for each taxonomic group from each provenience was also calculated, using the highest estimate available from counts of single, paired,[94] or multiple elements. However, for the analyses presented in this study, I use only the MNI for specimens identified to the species level, or to the genus level when no species of that genus were identified from the same provenience (*see* Table 37).

General Characteristics of the Lo Demás Fish Remains

This section covers taxonomy, habitat, and use of the fish taxa identified at Lo Demás. Table 35 provides a taxonomic chart of these fish. All of the species[95] inhabit the cool waters of the Humboldt

Table 37.—*Total NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals) by taxon for all analyzed fish samples from all stratigraphic complexes in Lo Demás (sample includes Subunits A1, A2, A3, B3, C3, 3B, and 10D in Sector I; Subunit 26D in Sector IV). MNI was aggregated by provenience and was calculated only for taxa identified to the genus or species level. A dash indicates that MNI was not calculated because of taxonomic level.*

	NISP	MNI
SQUALIFORMES	8	—
CLUPEIFORMES	9	—
Clupeidae	784	—
Brevoortia maculata	335	57
Sardinops sagax	2,582	456
Engraulidae	121	—
Engraulis ringens	2,253	624
Anchoa nasus	3	2
SILURIFORMES	—	—
Ariidae	1	—
PERCIFORMES	1	—
Haemulidae	12	—
Anisotremus sp.	77	26
Sciaenidae	219	—
Cynoscion analis	23	14
Paralonchurus peruanus	209	73
Sciaena sp.	389	92
Mugiloididae	16	—
Mugiloides sp.	17	7
Scombridae	33	—
Sarda sarda chiliensis	8	4
Centrolophidae	2	—
Medium size unidentified fish	302	—
Small size unidentified fish	302	—
Total	7,706	1,355

Table 38.—*Habitats and ranges of fish species identified from Lo Demás. Data from Mariano A. (1984) and Sánchez (1973).* [a] *The Peru or Humboldt Current flows north along the coasts of Chile and Peru until it reaches far northern Peru in the vicinity of Talara/Tumbes. Species with ranges listed as Peru Current are found throughout most of this area, unless a more limited area is defined.*

Species	Habitat
CLUPEIFORMES	
Brevoortia maculata	coastal pelagic
Sardinops sagax	coastal pelagic
Engraulis ringens	pelagic
Anchoa nasus	coastal pelagic
PERCIFORMES	
Anisotremus sp.	sandy/rocky benthic
Cynoscion analis	sandy/rocky benthic
Paralonchurus peruanus	benthopelagic
Sciaena sp.	sandy benthic
Mugiloides sp.	sandy/rocky benthic
Sarda sarda chiliensis	coastal pelagic

Species	Range
CLUPEIFORMES	
Brevoortia maculata	Peru (Peru Current)[a]
Sardinops sagax	Peru Current
Engraulis ringens	Peru Current
Anchoa nasus	transitional zone (North Peru/South Ecuador) and south into Peru Current
PERCIFORMES	
Anisotremus sp.	Peru Current
Cynoscion analis	Peru Current, north into transitional zone
Paralonchurus peruanus	transitional zone, south into Peru Current
Sciaena sp.	Peru Current along north and central coasts of Peru
Mugiloides sp.	Peru Current along south and central coasts of Peru
Sarda sarda chiliensis	Peru Current

Current, though some are more abundant in the transitional zone of northern Peru/southern Ecuador (Table 38), which corresponds to Olsson's (1961: 37–40) Paita Buffer Zone between the Panamic–Pacific and Peruvian Molluscan Provinces (*see* note 81). Of course, the comparative sample included only taxa found in the Chincha area today, and the unidentified specimens could well include exotic fish.

Also due to the restrictions of our comparative collection (and for the reasons outlined in the section on Methodology), all of the identified taxa inhabit the coastal pelagic zone, the sandy/muddy benthic zone, or the benthic sandy/rocky zone. However, the distribution of the comparative sample did not predict the overwhelming abundance of pelagic species in the remains, as determined by both Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) (*see* Table 37). The pelagic (free-swimming) species represent 87.9% of the sample by NISP and 84.4% by MNI aggregated by provenience, based only on those specimens identified to the genus or species level.

The dominance of herbivorous, schooling pelagic fish—primarily sardines (*Sardinops sagax*) and *anchovetas* (*Engraulis ringens*)—in the Lo Demás sample probably resulted from the fishing technology employed by the Chincha fishermen; this technology is related, in turn, to the probable purpose of Chincha fishing—to acquire fish for tribute and trade as well as for subsistence. The excavated deposit at Lo Demás contained many net fragments but only one fishhook (*see* Chapter 8). In general, benthic species are caught with hooks, often from the shore, whereas herbivorous, schooling pelagic species are netted from the shore or from boats or rafts (Wing and

Brown, 1979:95). Thus, the fish remains from Lo Demás support the artifactual evidence indicating that the Chincha fishermen made most of their capture by netting. The "Aviso" (Rostworowski, 1970: 170) says that the Chincha fishermen went to sea "each with his raft and *nets*" (emphasis added), confirming the archaeological indications of the predominant technology.

Net fish serve industrial purposes better than hook fish, as they can provide a higher biomass in return for effort. Modern industrial fisheries, such as that which fueled the Peruvian fish boom in the 1950s and 1960s, rely exclusively on netting. Hook fish tend to be larger, providing more meat per "package," and in Peru today, they are considered better eating (e.g., the drums, Family Sciaenidae, including corvina). The predominance of pelagic net fish in the Lo Demás sample and the use of nets by the Chincha fishermen therefore suggest that late pre-Hispanic Chincha fishing had industrial ends,[96] in accordance both with the documentary evidence for the organization and scale of the fishing community (*see* Chapter 2) and with the archaeological evidence for fish salting and/or drying at Lo Demás.

In addition to the posthole pattern and the matting associated with salt crystals and fish scales (*see* Chapter 6), there is another, tentative line of evidence for fish salting at Lo Demás. Altamirano (1984) precipitated salts from the periosteum of fish bones and terrestrial animal bones from the 1983 excavations and found a visually greater amount of salt from the fish bones than from most of the animal bones. Although further work is necessary to assess the significance of this result,[97] the greater amount of salt on the fish bones suggests that the fish were salted.

The evidence for pre-Hispanic fish salting at Lo Demás has special importance, because of recent assertions that Andean fishermen did not salt fish before the arrival of the Spaniards (Marcus, 1987*a*: 397, 1987*b*:53, 56). Not only the Lo Demás archaeological data, but also the ethnohistoric record argue for pre-Hispanic salting. Rostworowski (1981: 118) cites a 1549 *visita* which mentions salt fish as tribute, and Masuda (1982:102) discusses the documentary evidence for three classes of fish preservation: in the sierra, fish was "freeze-dried," like chuño; on the Peruvian north coast and in northern Chile, fish was dried in the sun; and on the Peruvian south coast, fish was salted and dried. The coastal distribution of salting and drying versus simply drying may be related to the distribution of winter "garúa" (dense, permanent fog). Chincha is in the "garúa" zone, where salting would be expected.

The presence of a full range of skeletal elements shows that the fishermen consumed some of their catch, in addition to fishing for tribute and trade. In terms of the relative importance of the two uses of fish (industrial and domestic), the high percentage of whole heads and cranial elements in the sample (far more than the number of vertebrae would warrant) supports the idea that many of the fish were processed but not consumed at the site (*see* Tables 39 and 40).[98] Preparation of fish for long-distance trade should involve removing their heads and possibly their tails. Ethnographic observations of the Maori in New Zealand support this assumption: these observations led Shawcross (1967) to suggest that a predominance of fish heads in a prehistoric midden from New Zealand indicates preservation and transportation off-site of the rest of the fish.

None of the bones show signs of cultural modification, indicating that consumption and/or production for exchange or other purposes constituted the primary uses of fish at Lo Demás.

Quantitative Analysis

Objectives and limitations. —The quantitative analysis of fish remains can provide information on a number of topics: dietary contribution of the fish, production vs. consumption, fish processing techniques, and changing patterns of fish exploitation.

As with mollusks, dietary reconstruction from fish remains involves estimation of the original fish meat weight represented by the archaeological remains. Modern techniques for estimation are similar to those for mollusks in relying on allometric modelling and regression analysis (e.g., Casteel, 1976). Reitz et al. (1987) provide an up-to-date overview of allometry and meat weight analysis, with considerable attention to fish. The method has great promise, but experimental data for Peruvian species are not yet available. For this reason, and because of the lack of formulae for Peruvian terrestrial mammals and the methodological difficulties in estimating food value from botanical remains, I do not attempt to quantify the dietary contribution of fish to Lo Demás subsistence. Such an attempt would face several additional problems. First, the use of ¼″ screen has biased the sample in ways that cannot be estimated until the fine-screen analyses are complete. Second, I have no secure way to determine which of the fish bones came from fish consumed

Table 39.—*NISP (Number of Identified Specimens) of fish from Lo Demás by skeletal element and sector (sample includes Subunits A1, A2, A3, B3, C3, 3B, and 10D in Sector I; Subunit 26D in Sector IV). Data compiled from Mariano A. (1984, 1985, 1986). A dash indicates that a given element was not present in a sector. This table includes all specimens identified by skeletal element, regardless of taxonomic level. Cranial elements are marked with an asterisk.* [a] *The results for branchia underestimate the amount present in the site, because these elements tended to disintegrate on excavation; field notes indicate several large concentrations of branchia in Sector I, although none were noted in Sector IV.*

	Sector I		Sector IV	
Element	NISP	%	NISP	%
cranium*	84	1.4	5	0.3
neurocranium*	199	3.4	15	0.8
frontal*	72	1.2	—	—
parietal*	10	0.2	8	0.4
preoperculum*	190	3.2	—	—
parasphenoid*	24	0.4	8	0.4
exoccipital*	24	0.4	—	—
supraoccipital*	3	0.1	—	—
quadrate*	6	0.1	—	—
premaxillary*	3	0.1	1	0.1
maxillary*	532	9.0	66	3.7
dentary*	958	16.2	328	18.3
articular*	8	0.1	—	—
operculum*	623	10.5	134	7.5
suboperculum*	141	2.4	21	1.2
hyoid arch*	4	0.1	—	—
branchial arch*	190	3.2	9	0.5
shoulder girdle	7	0.1	—	—
cleithrum	253	4.3	75	4.2
pelvic girdle	12	0.2	—	—
basipterygoid	4	0.1	—	—
vertebral column	13	0.2	6	0.3
precaudal skeleton	10	0.2	2	0.1
precaudal vertebra	663	11.2	687	38.3
caudal skeleton	23	0.4	1	0.1
caudal vertebra	1,130	19.1	280	15.6
urophoral bones	204	3.5	—	—
otolith*	58	1.0	38	2.1
hyomandibular*	444	7.5	111	6.2
pharyngeal teeth*	6	0.1	—	—
branchial spines*[a]	13	0.2	—	—
Total NISP	5,911		1,795	

Table 40.—*Cranial versus postcranial elements of fish by sector from the Lo Demás sample, expressed as NISP (Number of Identified Specimens). Table 39 indicates which elements were considered as cranial or postcranial. Percentages refer to the proportion of cranial and postcranial elements in each sector (i.e., percentages read down, not across). The difference in the fraction of cranial elements observed in the two sectors is 14.45 standard deviations greater than the expected difference (0) under the null hypothesis that the two samples were drawn from the same parent population; statistically, the observed difference is extremely significant.*

	Sector I	Sector IV	Total
Cranial	3,592 60.8%	744 41.4%	4,336
Postcranial	2,319 39.2%	1,051 58.6%	3,370
Total	5,911	1,795	7,706

at the site and which came from specimens prepared for export.

The patterning of skeletal elements in an archaeological site can provide insight into prehistoric fish processing techniques and the question of production vs. consumption. Analysis of this patterning requires that each bone be classified by skeletal element and taxon, counted, and summed at each hierarchical level of provenience (provenience, complex, sector, site). As mentioned above, a predominance of cranial elements may indicate that fish heads were removed from the rest of the fish as part of the process of preparing preserved fish for export. An alternate interpretation (in addition to the bias introduced by screen size) is that the vertebrae of small fish were consumed by the site's inhabitants along with the flesh. At Lo Demás, however, the large number of vertebrae recovered (though far too few to account for the MNI indicated by the cranial elements) demonstrates that if such a practice took place, it was not universal. The bones alone cannot determine which of the alternatives is correct; other classes of data are necessary.

Finally, recognition of changing patterns of fish use requires calculating the relative frequencies of different species through time in a stratified archaeological deposit. As with the mollusks, identifying and counting the sample is straightforward; problems arise at the interpretive stage because of the difficulty in assessing cultural preference vs. natural availability in midden formation (*see above,* discussion of natural versus cultural changes in the section on Quantitative Analysis of mollusks). To differentiate some of the changes due to preference from some of those resulting from availability, I have used the same assumption as for the mollusks: *changes in frequency of species in a stratigraphic sequence reflect changes in availability rather than preference when all of the involved species remain well represented in the contrasting archaeological levels.*

The above assumption does not apply to contrasting frequencies between different parts of a site when the exact contemporaneity of the strata in each part of the site cannot be established. Interpretations based on such contrasts are more general and less secure than those drawn from changes within a sin-

Table 41.—Sardinops sagax *versus* Engraulis ringens, *Lo Demás Sector I, Stratigraphic Complexes A to D, by NISP and by MNI. Counts are absolute, percentages are relative to all fish remains from each stratigraphic complex. Compare to Fig. 56, which plots* Sardinops *against* Engraulis *for Complexes B to D.*

	A		B		C		D	
	NISP	%	NISP	%	NISP	%	NISP	%
S. sagax	7	35.0	172	17.2	750	27.3	1,194	55.7
E. ringens	0	0.0	363	36.3	1,032	37.6	472	22.0
	MNI	%	MNI	%	MNI	%	MNI	%
S. sagax	1	25.0	17	14.8	69	22.2	147	52.9
E. ringens	0	0.0	81	70.4	210	67.5	121	43.5

gle stratigraphic sequence. Even when contemporaneity of strata is clear, different functional contexts of different parts of a site introduce new possibilities for cultural explanations of contrasting frequencies. As with the mollusks, comparison of the fish assemblages from Sector I (common residences) and Sector IV (elite structures) of Lo Demás provides a case in point (*see below*).

Analysis by stratigraphic complex in Sector I.—For this analysis, the different members of each stratigraphic complex in Sector I were pooled into complex totals, in order to see changes through time in predominant fish taxa (Sandweiss, 1989:Tables 47–50).

One major change takes place in the stratigraphic sequence in Sector I: in the latest Complex, D, sardines (*Sardinops sagax*) replace *anchovetas* (*Engraulis ringens*) as the dominant species in terms of both NISP and MNI (Table 41, Fig. 56). Anchovetas had dominated the fish remains in two lower complexes (B and C). This shift parallels the change in the shell remains from *Donax* to *Semimytilus* predominance between Complexes C and D.

As with the mollusks, the differences in the frequencies of sardines and *anchovetas* between Complexes C and D are, in statistical terms, almost certainly due to real differences in the parent populations and are not the result of random variation (*see* Table 42). This result holds true for the fish when compared by NISP, MNI aggregated by complex, and MNI aggregated by provenience. The difference between Complexes B and C (in both of which anchovetas dominate) for NISP is statistically significant, as it was for the mollusks. For MNI aggregated either by complex or by provenience, however, the difference between B and C is much less significant ($P > 0.10$ and $P > 0.20$, respectively). In other words, not only is the difference between C and D (the sardine/*anchoveta* reversal) large and real, but B and C are much more similar to each other than either is to D.

In accordance with the assumption about changes in species frequencies, the sardine/*anchoveta* reversal represents a change in the availability of these species rather than in dietary preference. However, interpretation of the change presents greater ambiguities than did the shift in shells, because fish are not restricted to such narrowly defined habitats as are mollusks. The fact that the frequencies of *anchovetas* and sardines change concurrently with the molluscan frequencies argues against a natural change limited to the shoreline as the explanation, while the molluscan data argue against climate change—which *can* affect the relative abundance of sardines and *anchovetas*. The key question, then, is whether the construction of a pier (as suggested by the molluscan data)—or the motives underlying such a project—might mediate a technological or cultural alteration in the relative availability of these fish. Although both species can be found together near the shore, sardines range farther offshore than do *anchovetas* (Mariano, 1984). A pier would allow the use of larger craft capable of going further out to sea for more time than the *caballitos* (small, single person fishing rafts traditionally used by Andean fishermen) that can be launched from the shore. However, both sardines and *anchovetas* are often reported together, and both can be taken close to the shore with a similar net-fishing technology. Despite this ambiguity, the exact concurrence in the reversal of dominant species of both phyla (mollusks and fish) supports a culturally mediated cause of change in availability (not in preference) and thus supports the "pier" hypothesis proposed on the basis of the molluscan data.

Analysis by sector.—The samples of fish remains from Sectors I and IV of Lo Demás are similar in broad outline, but show a number of interesting

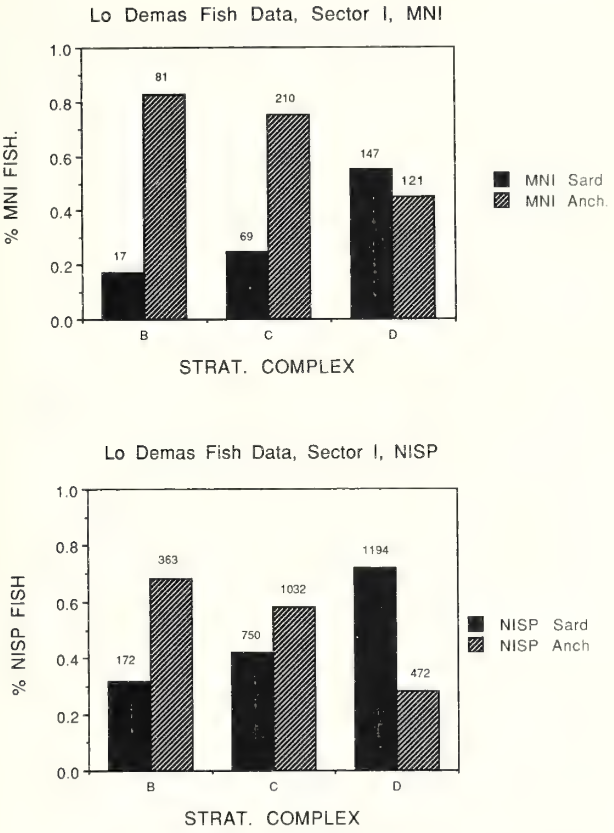

Fig. 56.—Relative abundance of sardines (*Sardinops sagax*) and *anchovetas* (*Engraulis ringens*) in the sample from Stratigraphic Complexes B, C, and D in Sector I of Lo Demás, by MNI and by NISP. Histograms show percent of sardines and *anchovetas* in each level; in calculating the percentages, only these two species were used. The numbers above the histograms show the absolute abundance of each species in each complex.

differences at a more detailed level (Tables 39, 40, 43, 44, 45).

Relative to Sector I, Sector IV has a significantly higher percentage of Clupeiformes relative to Perciformes among the specimens identified to genus or species (Table 45). Most Clupeiformes are small, herbivorous, schooling, pelagic fish usually caught with nets; at Lo Demás, sardines (*Sardinops sagax*) and *anchovetas* (*Engraulis ringens*) dominate this taxonomic order.[99] The Perciformes are larger and at Lo Demás are represented primarily by drums (*Paralonchurus peruanus* and *Sciaena* sp.) and a grunt (*Anisotremus* sp.).[100] Most of the Perciformes at Lo Demás are benthic species best caught with hooks. Both Clupeiformes and Perciformes can be caught close in to the shore (E. Reitz, personal communication, 1988). As Table 45 shows, Perciformes make up a much higher percentage of those remains identified to genus or species level in Sector IV (24.1%) than in Sector I (9.3%). In Peru today, the Perciformes are preferred to the Clupeiformes for eating, because of their size, lower ratio of bones to flesh, and the quality of their flesh. The higher frequency of Perciformes in Sector IV suggests that the elite inhabitants of Lo Demás had privileged (differential) access to preferred species, a hypothesis supported by the molluscan data (*see above*).

Table 42.—*Statistical analysis of the variation in frequency of* Sardinops sagax sagax *(sardine) relative to* Engraulis ringens *(*anchoveta*) between stratigraphic complexes in Sector I, Lo Demás. Analyses were run on the data for the NISP, MNI aggregated by stratigraphic complex (SC), and MNI aggregated by provenience (pr.). Results are reported as the observed difference in the percentage of* Sardinops *between two levels expressed as standard deviations from the expected difference (0) based on the null hypothesis that each pair of complexes was drawn from the same parent population.*

Between Complexes	Number of Standard Deviations		
	NISP	MNI (SC)	MNI (pr.)
C and D	17.50	7.21	6.85
B and C	4.12	1.27	1.56

Table 43.—*Fish remains from Sector I, Lo Demás (sample includes Subunits A1, A2, A3, B3, C3, 3B, and 10D), expressed as NISP (Number of Identified Specimens) and as MNI (Minimum Number of Individuals) aggregated by provenience (pr.), stratigraphic complex (SC), and sector total (Sr.); MNI is provided only for taxa identified to the species level, or to the genus level if no species of that genus is present. A dash means not applicable.*

Taxon	NISP	MNI (pr.)	MNI (SC)	MNI (Sr.)
Order Squaliformes	8	—	—	—
Order Clupeiformes	9	—	—	—
Family Clupeidae	252	—	—	—
Brevoortia maculata	287	46	18	15
Sardinops sagax	2,123	326	234	233
Family Engraulidae	121	—	—	—
Engraulis ringens	1,867	488	412	412
Anchoa nasus	3	2	1	1
Family Ariidae	1	—	—	—
Order Perciformes	1	—	—	—
Family Haemulidae	9	—	—	—
Anisotremus sp.	46	18	4	3
Family Sciaenidae	180	—	—	—
Cynoscion analis	18	10	3	2
Paralonchurus peruanus	146	38	16	14
Sciaena sp.	211	59	16	14
Family Mugiloididae	16	—	—	—
Mugiloides sp.	11	5	2	1
Family Scombridae	33	—	—	—
Sarda sarda chiliensis	8	4	2	1
Family Centrolophidae	2	—	—	—
Medium-sized unidentified fish	260	—	—	—
Small-sized unidentified fish	299	—	—	—
Total	5,911	996	708	696

Table 44.—*Fish remains from Sector IV, Lo Demás (Subunit 26D), expressed as NISP (Number of Identified Specimens) and as MNI (Minimum Number of Individuals) aggregated by provenience (pr.) and sector (Sr.); MNI is provided only for taxa identified to the species level, or to the genus level if no species of that genus is present. A dash means not applicable.*

Taxon	NISP	MNI (pr.)	MNI (Sr.)
Order Clupeiformes			
Family Clupeidae	532	—	—
Brevoortia maculata	48	11	3
Sardinops sagax	459	81	48
Engraulis ringens	386	139	120
Order Perciformes			
Family Haemulidae	3	—	—
Anisotremus sp.	31	8	2
Family Sciaenidae	39	—	—
Cynoscion analis	5	4	1
Paralonchurus peruanus	63	29	18
Sciaena sp.	178	35	13
Mugiloides sp.	6	2	1
Medium-sized unidentified fish	42	—	—
Small-sized unidentified fish	3	—	—
Total	1,795	309	206

A second pattern which emerges from the fish data is the significant difference in the proportion of cranial versus post-cranial elements between Sectors I and IV (*see* Tables 39, 40); Sector IV has a much lower frequency of cranial elements. Considering the probable relationship between a high proportion of cranial elements and the preparation of fish for export (*see above*), the lower frequency of cranial elements indicates that consumption and not fish processing was the primary Sector IV use of fish (to the extent that the Subunit 26D can be taken as representative of the sector). The lack of nets and other features directly related to fishing and fish-processing (except for one possible bone *mallero*) supports this interpretation (*see* Chapters 6 and 8).

Table 45.—*Comparison of Clupeiformes versus Perciformes fish by NISP between Sectors I and IV, Lo Demás (sample includes subunits A1, A2, A3, B3, C3, 3B, and 10D in Sector I; Subunit 26D in Sector IV). Percentages refer to the proportion of Clupeiformes and Perciformes in each sector (i.e., percentages read down, not across). Results are reported in Part c as the observed difference in the percentage of Clupeiformes between the two sectors expressed as standard deviations from the expected difference (0) based on the null hypothesis that the samples from both sectors were drawn from the same parent population. Although the difference is greater for the data limited to generic or specific identification, the difference in both cases is statistically highly significant.*

a) Data for specimens identified to the genus or species level

Order	Sector I	Sector IV	Total
Clupeiformes	4,280	893	5,173
	90.7%	75.9%	
Perciformes	440	283	723
	9.3%	24.1%	
Total	4,720	1,176	5,896

b) Data for specimens identified to the order, family, genus, or species level

Order	Sector I	Sector IV	Total
Clupeiformes	4,662	1,425	6,087
	87.3%	81.4%	
Perciformes	681	325	1,006
	12.7%	18.6%	
Total	5,343	1,750	7,093

c) Observed difference in percentage of Clupeiformes between Sectors I and IV

Identification Level	# of Standard Deviations
Genus/Species (A)	13.80
Order-Species (B)	6.06

The final comparison between Sectors I and IV concerns stratigraphic changes in relative abundance of sardines and *anchovetas*. The proportion of sardines relative to *anchovetas* throughout the sequence in Subunit 26D does not correlate unambiguously with the *Donax*/*Semimytilus* proportions. The molluscan data show a shifting *Donax*: *Semimytilus* ratio tentatively correlated with Complexes B/C and D in Sector I (*see above*). The pattern for the fish in Subunit 26D is much less regular—the predominant species (by NISP)[101] changes twelve times from bottom to top of the sequence. Much of this noise disappears when only strata with NISP counts of 25 or greater are used (five reversals; *see* Fig. 57). However, the pattern which emerges contradicts the tentative correlation between sectors based on mollusks. A reversal occurs within the proveniences which, according to the molluscan data, should correspond to Complex D in Sector I; in most of the proveniences which should correspond to Complexes B and C, sardines predominate. In these complexes in Sector I, *anchovetas* were the dominant species. The correlation based on mollusks may be wrong, but the ceramics and (to a degree) the carbon-14 dates indicate that the two sectors are at least roughly contemporaneous. The lack of correlation of the fish and molluscan remains may well be due to the different functional contexts of the two deposits. The need for large quantities of *anchovetas* and sardines for processing in Sector I would have linked the inhabitants of this sector more closely to fluctuations in availability, while the privilege of selection (differential access) for consumption enjoyed by the Sector IV elites would have insulated them from variations in abundance. There is no

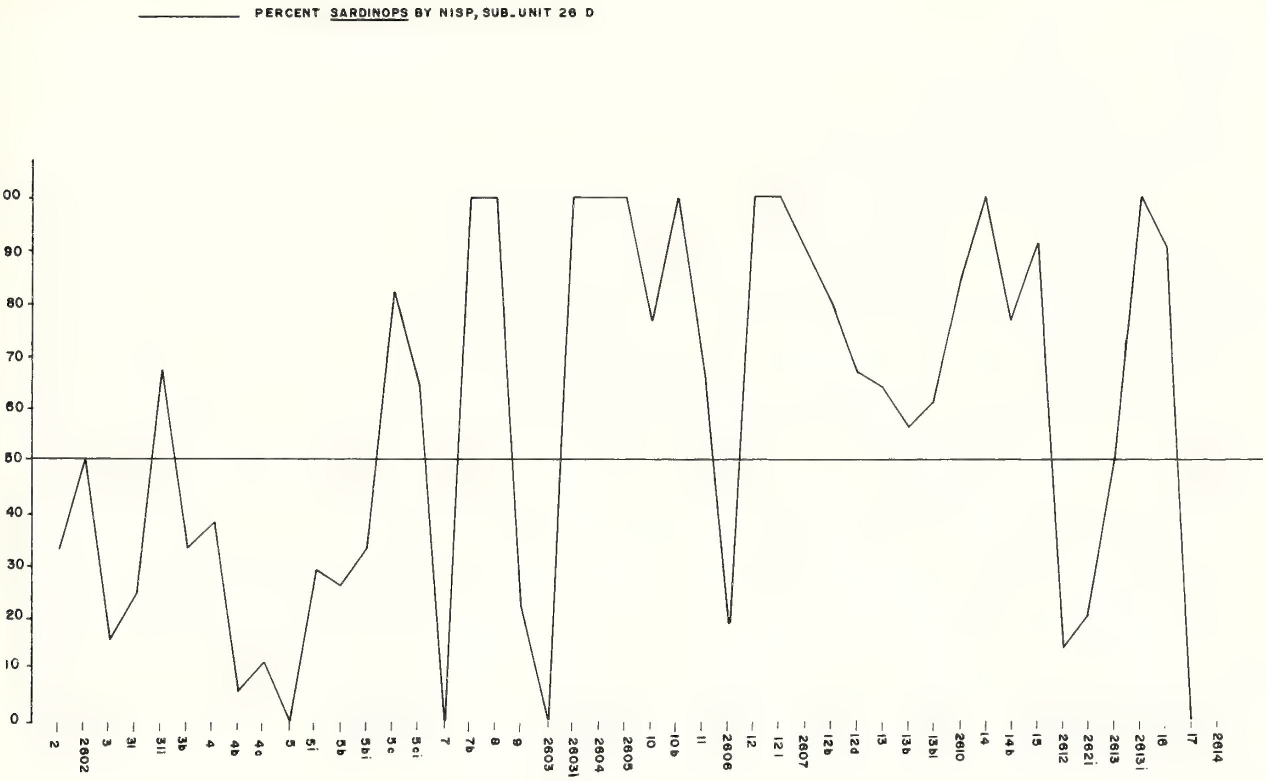

Fig. 57.—Percent of sardines (*Sardinops sagax*) relative to *anchoveta* (*Engraulis ringens*) by level in Lo Demás, Sector IV, Subunit 26D, for NISP. Only levels with a NISP of 25 or greater are shown.

evidence that mollusk meat was produced for export, so the mollusks would not have been subject to the same constraints.

CRUSTACEANS

Lo Demás did not contain many crustaceans; the few remains tended to be small bits of crab carapace or claws (barnacles—also rare—were analyzed with the mollusks). A. Kameya K. (Instituto del Mar del Peru, Callao) identified the larger pieces from the 1983 excavation; given the limited nature of the remains, I use only the presence/absence criterion in analyzing these data. Crab remains from the 1984 excavations have not yet been studied. The 1983 crustaceans came from eleven proveniences within Complex D and one provenience within Complex C (Complex B was not present in the 1983 excavations). In addition, one specimen came from the surface debris covering Complex D.

Pieces of a purple crab (*Platyxanthus* sp., probably *P. orbignyi*) were identified in ten of the eleven proveniences from Complex D and in the Complex C provenience. *Platyxanthus* is a medium-sized crab which lives along the shore from the intertidal zone to about 25 m depth and ranges along the Andean coast from San Antonio, Chile, to Salaverry, Peru (Mendez, 1982), or possibly Ecuador (Sánchez Romero, 1973:364). Rock crabs of the family Grapsidae were also identified in four of the Complex D proveniences. Chirichigno (1970) lists 17 Peruvian species of Grapsidae.

The crab remains provide little information about the use of crustaceans by the inhabitants of Lo Demás; they do provide some data on the marine environment at the time of occupation. In a study of the utility of arthropod chitin in paleoenvironmental reconstruction, Arndt Schimmelmann ran stable isotope analyses ($\delta\ ^{13}C$, $\delta\ ^{15}N$, $\delta\ ^{18}O$, and δ D) on chitin in *Platyxanthus* specimens from seven of the 1983 proveniences at Lo Demás (Schimmelmann et al., 1986:562) (*see* Fig. 58). Although Schimmelmann did not have modern samples of *Platyxanthus orbignyi* for comparison, he and his colleagues found that the results for the archaeological samples closely resembled data on the Peruvian lobster *Panulirus gracilis*, which lives in a habitat similar to that of *Platyxanthus* (Schimmelmann et al., 1986). These data suggest that marine climatic conditions at

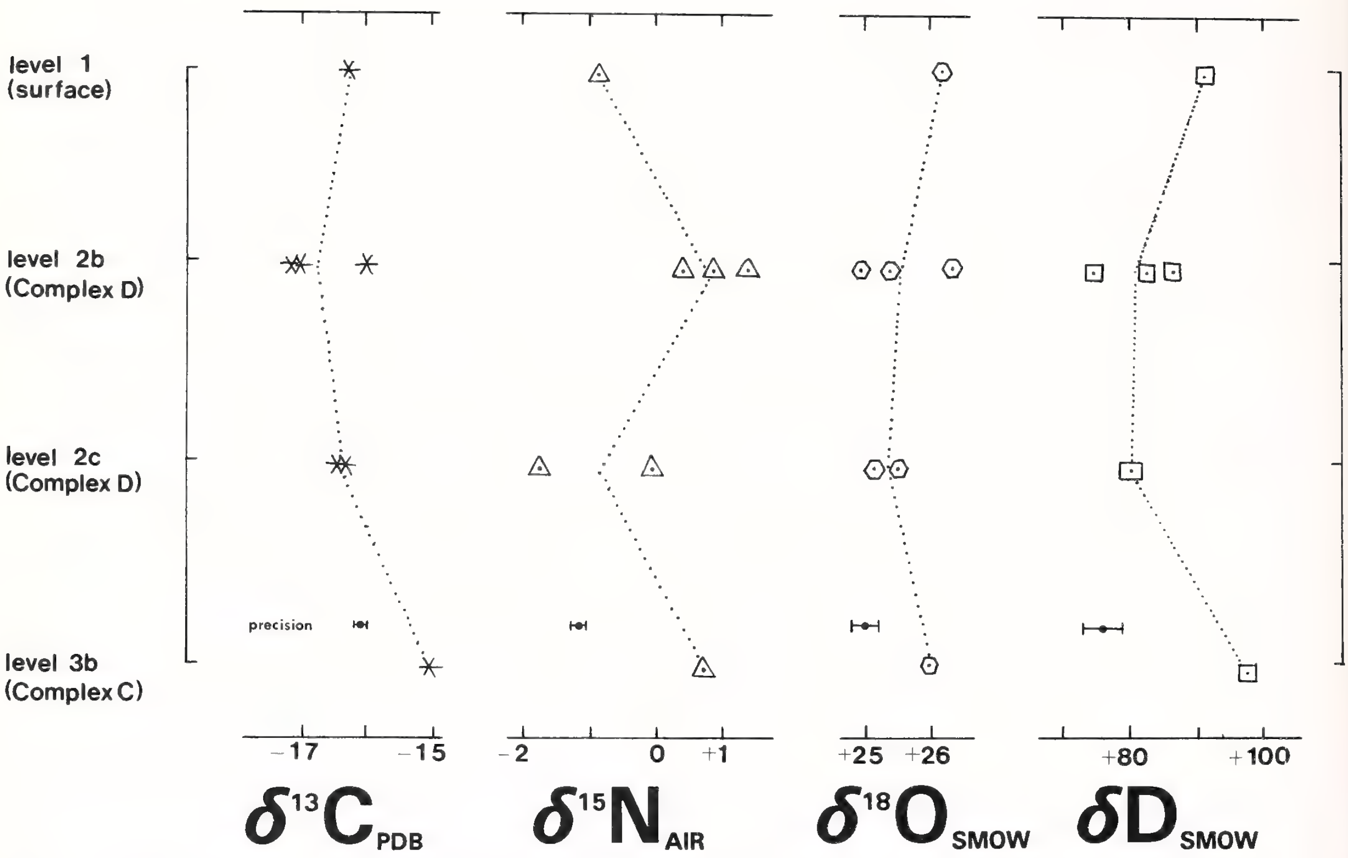

Fig. 58.—Data on stable isotope analyses of crab chitin from Lo Demás. Adapted from Schimmelmann et al. (1986:562).

Chincha in the Late Horizon closely resembled modern conditions on the Peruvian coast.

Fig. 58 shows very similar results for δ ^{13}C, δ ^{18}O, and δ D between the two Complex D proveniences and noticeable differences in δ ^{13}C and δ D between the Complex D proveniences and the Complex C provenience. This trend could indicate a slight change in the marine environment between the two complexes, at the same time as the *Donax/Semimytilus* and *Sardinops/Engraulis* reversals occur. However, Schimmelmann (personal communication, 1985) writes that

> "I am very skeptical about the significance of the small isotopic differences between the levels. My interpretation is the following: "All samples from all levels measured (for all isotope ratios) show a remarkably *constant* signal which excludes large environmental changes, especially large fluctuations in the influx of terrestrial carbon as [a] food source, and in the isotopic composition of the water where the animals lived. No direct conclusion can be reached about constancy of temperature at the site. The observed isotopic variabilities are in the ranges of natural variabilities within populations of individuals from *one* modern site."

Thus, the isotopic data from the Lo Demás crab chitin support the suggestion from the mollusk and fish data that climate change between Complexes C and D does not account for the *Donax/Semimytilus* and *Sardinops/Engraulis* reversals.

VERTEBRATE REMAINS OTHER THAN FISH

Non-fish vertebrates recovered from Lo Demás include birds, sea mammals, and land mammals (including *Homo sapiens*).[102] In comparison with the fish and mollusks, remains of these animals are scarce and therefore offer more limited information.

The faunal remains covered in this section come from the same primary midden contexts as the fish and mollusks. The studied sample includes all of the bones recovered in the ¼″ screen from the 1983 test excavations (Sector I), from Subunits 3B and 10D (Sector I), and from Subunit 26D (Sector IV) Subunit 26D was treated as a single stratigraphic complex.

Alfredo Altamirano E. (Laboratorio de Paleoetnozoología, San Marcos University, Lima, Peru) identified the remains covered in this section (Altamirano E., 1984, 1986). Lacking extensive comparative collections, the specific identifications of fauna other than large terrestrial mammals and guinea pigs (*Cavia porcellus*) should be considered as tentative. Altamirano identified 712 (57.5%) of the 1,238 bones in the sample to the genus or species level. Another 185 specimens (14.9%) could be classified to the family level or as bird, sea bird, marine mammal, mammal, turtle, or lizard. Only 336 (27.1%) of the bones came from the Sector I sample; the rest (902) came from Subunit 26D in Sector IV.

Table 46 lists the families, genera, and species of the identified bones, along with their common names. Most of the birds would have lived along the shore or in the marshy ground that lay between Lo Demás and the beach (*see* Chapter 5), as would the frogs and turtles. The doves, or palomas (*Zenaida* sp.) live in the valley. The wild rodents (unidentified mouselike rodents) were probably endemic to all coastal areas of human occupation, while the animal coprolite evidence (*see below*) shows that the domesticated guinea pigs (*Cavia porcellus*) lived with the site's human inhabitants. Furthermore, the intact or nearly intact bodies of seven guinea pigs were found in the Sector I deposits. The animal coprolite evidence also shows that camelids were brought live to Sector IV but not to Sector I. This limited distribution, and the apparent function of camelids as beasts of burden, argue in favor of the camelids being domesticated. The marine mammals generally live along rocky shores and were probably brought to Lo Demás from the same areas as some of the imported mollusks, i.e., Paracas, the Chincha islands, and/or possibly the coast between Jahuay and Cañete.

Table 46.—*List of vertebrate taxa other than fish identified from Lo Demás. Data from Altamirano E. (1984, 1986).*

- Aves
  - Pelecanidae
    - *Pelecanus* sp. (pelican)
  - Phalacrocoracidae
    - *Phalacrocorax* sp.
  - Sulidae
    - *Sula variegata*
  - Columbidae
    - *Zenaida* sp.
  - Laridae
    - *Larus belcheri*
- Mammalia
  - Hominidae
    - *Homo sapiens* (human)
  - Cricetidae
    - unidentified small mouse
  - Caviidae
    - *Cavia porcellus* (guinea pig)
  - Canidae
    - *Canis* sp. (dog)
  - Mustelidae
    - unidentified otter
  - Otariidae
    - *Otaria* sp. (sea lion)
  - Camelidae
    - *Lama glama* (llama)
  - Cervidae
    - *Odocoileus virginianus* (white-tail deer)
  - Bovidae
    - *Bos taurus* (cow)
- Other
  - *Batrachophrynus* sp. (frog)
  - unidentified turtle
  - unidentified lizard

Five of the intact guinea pigs in Sector I are from Complex C and one each is from Complexes A and B. All of the examples had some fur, and several of them were so well preserved as to include whiskers. The presence of the fur and the generally intact nature of these guinea pigs shows that they were not eaten by the inhabitants of Lo Demás, though the presence of disarticulated *Cavia* bones (some charred) shows that other guinea pigs had been consumed. The stomach of one of the specimens from Complex C had clearly been slit (Fig. 59); the same may have happened with several of the others. *Curanderos* (healers) in the Andes today use guinea pigs as diagnostic tools by rubbing the live animal on the body of a patient and then slitting the guinea pig's stomach to study the entrails (e.g., Bolton and Calvin, 1981:315–316); guinea pigs used in this way are usually not eaten. Ethnohistoric data indicate that the same practice was carried out in late pre-Hispanic times (Alfredo Torero, personal communication, 1984). Guinea pigs were also used for sacrifices; Arriaga (1968 [1621]:210) wrote that

> "the ordinary sacrifice is of guinea pigs, of which they make evil use, not only for sacrifices but also to divine with them and to cure with them . . . . When they have to sacrifice them, sometimes they open them along the middle with the nail of the thumb. . . ."[103]

Polo (1906 [1559]:198) also wrote about the Andean practice of cutting open various animals—including guinea pigs—to study their entrails for good or bad omens; guinea pigs for sacrifice were to be domestic, not wild (Polo, 1906 [1559]:226).

The discovery in Lo Demás of intact guinea pigs with slit stomachs argues strongly for the presence

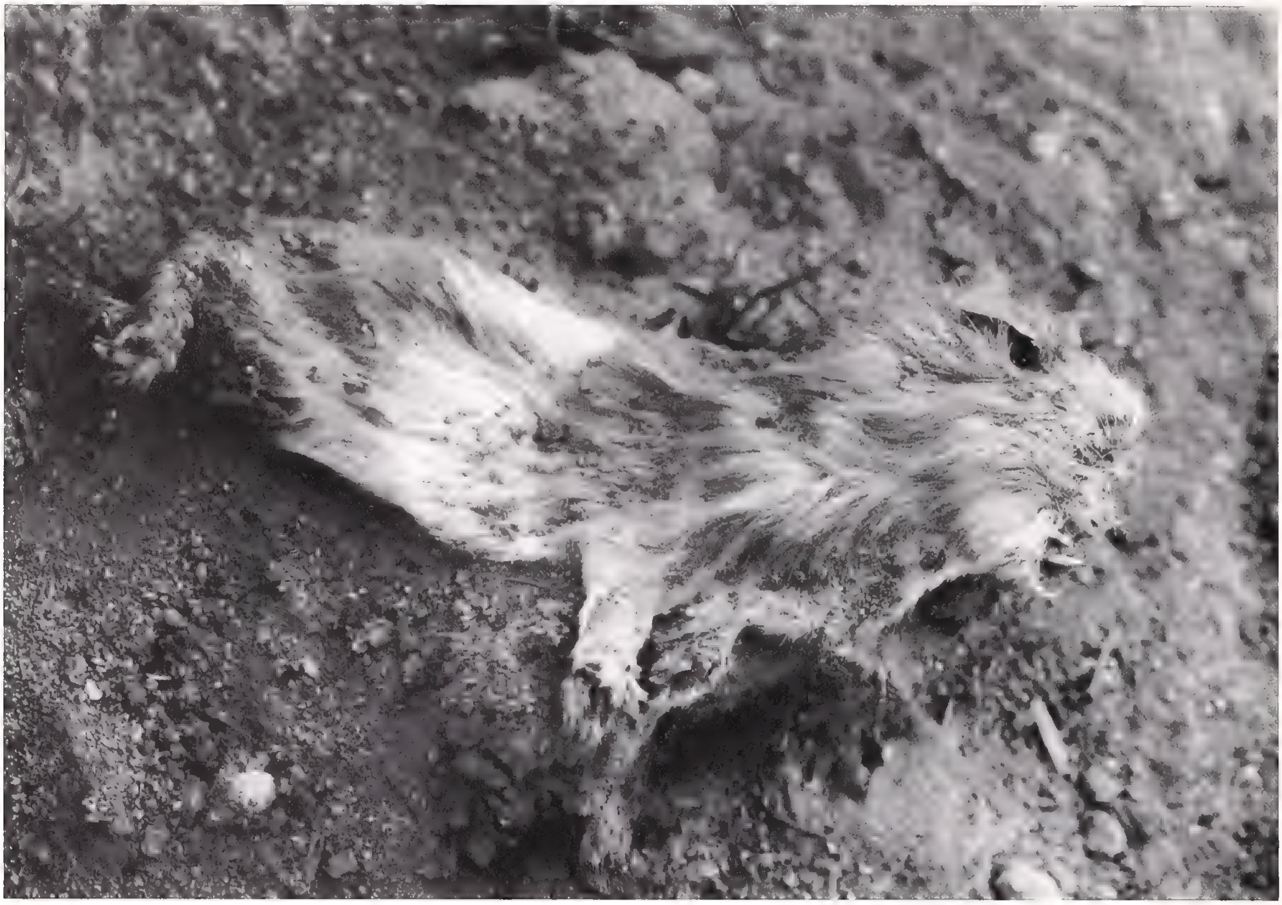

Fig. 59.—Guinea pig with slit stomach, Level 3–6, Subunit 3A, Complex C, Sector I, Lo Demás, Cat. 887.

of a *curandero* or ritual specialist at the site during the Late Horizon, though perhaps only during the time covered by Complexes A through C.

We also found an intact guinea pig underneath the child burial in Sector II. This specimen had been sacrificed by having its throat slit. The coarse components of the stomach contents of the adult human buried alongside the child contained 20% masticated dicot fibers and 15% *Capsicum annuum* (hot pepper) seeds (Jones, 1985, 1986), both of which may have had medicinal use (John G. Jones, personal communication, 1985). Although the data from the burials must be treated with caution until the graves can be securely cross-dated with the Late Horizon occupation in Sectors I and IV, they do provide further evidence for the presence of a *curandero* at Lo Demás.

During the excavation in 1983, we uncovered an intact bird body deliberately buried beneath a floor in Complex C (Fig. 15). Altamirano (1984) identified this bird as a grey-headed albatross (*Diomedea chrysostoma*). According to Tovar (1974), this species lives by robbing fish from other birds, and the fishermen may have considered it an important totemic symbol. Another intact bird (unidentified) was buried under an unexcavated wall in Complex C in the 1983 excavation area, and wall paintings of several seabirds were found in Room IV–1a in Building IV–1 in the elite Sector (IV) of Lo Demás (*see* Chapter 6, Figs. 16, 17). A piece of pyroengraved gourd from Sector I, Complex C, also has figures of birds (Chapter 8, Fig. 44), as does the copper tweezers from the Pachas collection (Chapter 8, Fig. 40).

The few bone artifacts from the excavations are treated in Chapter 8. Among the rest of the bones, modifications include charring and evidence of biting or gnawing. Several large bones from Subunit 26D in Sector IV showed cut marks, as did several bones from Sector I (*see* Sandweiss, 1989:Table 56).

Table 47 presents the NISP counts by stratigraphic complex (in Sector I), the Sector I totals, the Subunit 26D counts, and the site total.[104] Because of potential sample size and aggregation effects due to the small size of the sample (*vide* Grayson, 1984),

Table 47.—*NISP (Number of Identified Specimens) of vertebrate taxa other than fish from Lo Demás, listed by stratigraphic complex (in Sector I), by sector totals, and by site total (sample includes Subunits A1, A2, A3, B3, C3, 3B, and 10D in Sector I; Subunit 26D in Sector IV). Data from Altamirano E. (1984, 1986). A dash indicates no specimen.* [a] *The one specimen identified as probably* Bos taurus *is a small square of hide found near the surface of Stratigraphic Complex D. See text for discussion.*

Taxon	Complex				Sector Totals		Site Total
	A	B	C	D	I	IV	
Laridae	—	—	12	3	15	32	47
Larus belcheri	—	—	2	1	3	—	3
Larus sp.	—	—	2	—	2	—	2
Phalacrocoracidae	—	—	6	—	6	—	6
Phalacrocorax sp.	—	9	28	18	55	79	134
Pelecanus sp.	—	3	3	1	7	25	32
Sula variegata	—	1	2	11	14	5	19
Sula sp.	—	1	3	—	4	14	18
Zenaida sp.	—	—	1	13	14	1	15
unidentified seabird	3	6	22	12	43	—	43
small unidentified seabird	—	3	1	4	8	8	16
medium unidentified seabird	—	—	—	7	7	44	51
large unidentified seabird	—	1	—	—	1	—	1
unidentified bird	—	—	1	—	1	—	1
small unidentified bird	—	4	—	—	4	—	4
medium unidentified bird	—	2	2	—	4	—	4
large unidentified bird	—	—	1	—	1	—	1
Otariidae	—	—	1	—	1	—	1
Otaria sp.	—	—	—	—	—	21	21
unidentified otter	—	2	11	—	13	1	14
unidentified marine mammal	—	—	—	—	—	6	6
Camelidae	—	—	—	—	—	48	48
Lama glama	—	—	—	—	—	7	7
Lama sp.	—	—	—	—	—	11	11
Odocoileus virginianus	—	—	—	—	—	1	1
Canis sp.	—	1	1	—	2	—	2
Bos taurus[a]	—	—	—	1	1	—	1
Mustelidae	—	—	1	—	1	—	1
unidentified small mouse	10	16	14	34	74	247	321
Cavia porcellus	—	4	3	6	13	26	39
unidentified mouse	—	—	—	—	—	20	20
Cavia sp.	—	—	—	3	3	5	8
Homo sapiens	4	—	—	—	4	5	9
medium unidentified mammal	—	—	1	—	1	3	4
unidentified frog/toad	—	—	—	—	—	2	2
Batrachophrynus sp.	—	—	1	—	1	34	35
unidentified turtle	—	—	1	1	2	—	2
unidentified lizard	—	—	1	3	4	—	4
unidentified bones	—	11	4	12	27	257	284
Total	17	64	125	130	336	902	1,238

I do not list MNI for the non-fish bones. For these remains, MNI did not differ significantly from NISP when aggregated by provenience. The small size of the Sector I sample also precludes meaningful interpretations of the variation by stratigraphic complex within Sector I, but some interesting patterns are apparent in the contrasts between the samples from Sectors I and IV.

As Table 48 shows, birds (mostly seabirds) comprise the majority of the bones in Sector I, where they are almost twice as frequent as in Sector IV. Sea mammals have equal representation in the two zones, but the large terrestrial mammals (mainly camelids) are over four times as frequent in Sector IV. No camelid or cervid bones were present in Sector I, where the large terrestrial mammal sample consists of four human bones, two dog bones, one unidentified mammal bone, and a small piece of hide (probably cow) from a near-surface provenience in Complex D.[105] Many of the camelid bones in Sector IV are burnt, and some show cut marks (*see* Sandweiss, 1989:Table 56), indicating that the

Table 48.—*Comparison of vertebrate fauna other than fish between Sectors I and IV, Lo Demás, by major faunal category. Data compiled from Table 47. Completely unidentified bones (27 in Sector I, 257 in Sector IV) were not used in calculating the totals and percentages presented below.*

Faunal Category	Sector I NISP	Sector I %	Sector IV NISP	Sector IV %
birds	189	61.2	208	32.2
large land mammals	8	2.6	75	11.6
sea mammals	14	4.5	28	4.3
rodents	91	29.4	298	46.2
other	7	2.3	36	5.6
Total	309		645	

inhabitants of Sector IV ate camelid meat. The one cervid bone, a rib of the deer *Odocoileus virginianus,* also came from Sector IV (Subunit 26D) and shows cut marks. The bones thus provide further evidence for differential access to subsistence resources by the elite residents of Sector IV.

Rodent bones are significantly more common in Sector IV than in Sector I (Table 48), although domesticated guinea pig bones (*Cavia* sp. and *Cavia porcellus*) have about the same frequency in the two sectors (5.2% in Sector I, 4.8% in Sector IV). The difference comes with the wild rodents (24.3% in Sector I, 41.4% in Sector IV). Altamirano (1986) suggests that the wild rodents in the Lo Demás sample came to the site as scavengers, not as a hunted food source for the human inhabitants. If so, the difference between the sectors may indicate that the rodents found more food in Sector IV, perhaps due to more stored agricultural produce. However, the small size of the sample and the much larger number of unidentified bones in Sector IV[106] argue for caution in interpreting this statistic.

Animal Coprolites

Animal coprolites provide the final class of faunal data available from Lo Demás. In 1985, Jeffrey D. Klausner studied the animal feces from Subunit 10D in Sector I and Subunit 26D in Sector IV. He began by making a comparative collection of modern guinea pig, sheep, goat, llama, and burro feces. Sheep and goat were very similar, and as a group, the caprine (sheep/goat) sample included specimens that closely resembled some of the llama specimens. The difficulty in distinguishing between European and Andean domesticates is the major limitation on the utility of the coprolite data.

Animal coprolite specimens from Lo Demás were identified as sheep/goat, llama, guinea pig, and unknown.[107] Differences occur between the stratigraphic complexes in Subunit 10D (Sector I), and within the stratigraphic sequence in Subunit 26D (Sector IV), and between the samples from the two sectors.

In Sector I, guinea pig feces comprise almost the entire sample (Table 49a). Only two fragments were identified as llama feces and 29 specimens (1 whole, 28 fragments) were of unknown types. Nearly all of the coprolites came from Stratigraphic Complex B, while Complexes A and D have virtually no specimens. Future work with the Lo Demás remains will include studying a larger sample of animal coprolites to determine whether or not the stratigraphic distribution of these remains in Subunit 10D is representative of the rest of the excavated area. For the moment, the percentage of proveniences containing any animal coprolites in each stratigraphic complex (presence/absence) provides weak support for the pattern shown by the Subunit 10D sample (*see* Sandweiss, 1989:Table 60); both the percentage of proveniences with coprolites and the percentage of coprolites in 10D have the same rank order by complex.

The lack of guinea pig feces in Complex D correlates with the lack of guinea pig corpses in that complex. However, the studied sample of animal bones from Sector I contained more *Cavia* bones in Complex D than in Complexes A to C combined (of course, the total number of *Cavia* bones in Sector I samples was only 16; *see* Table 47). These data suggest that although guinea pigs were eaten during the occupation of Complex D, fewer (or no) live guinea pigs were kept in the excavated area of Sector I during that time. This pattern may indicate that the *curandero* who was present at the site during Complexes A through C was not there during Complex D.

In contrast to the sample from Sector I, the animal coprolites from Sector IV have a very high proportion of llama feces in addition to guinea pig specimens (Table 49b). Llama feces probably comprise the majority of the unidentified specimens from Subunit 26D. The presence of llama feces indicates that these animals came to Lo Demás alive; however, they were restricted to the monumental sector of the site. This contrast between the two sectors of Lo Demás provides another indication of the differential or privileged access to resources exercised by the elite inhabitants of Sector IV.

Although the Sector IV sample contains a few camelid bones (some with cut marks), the presence

Table 49.—*Animal coprolite data from Lo Demás. a) Summary of coprolite data from Subunit 10D in Sector I, by stratigraphic complex. b) Summary of coprolite data from Subunit 26D, Sector IV. A dash indicates not present.*

a) Subunit 10D, Sector I

	Guinea Pig		Llama		Unknown	
Complex	Whole	Fragment	Whole	Fragment	Whole	Fragment
A	2	—	—	—	—	—
B	2,975	357	—	1?	1	—
C	17	7	—	—	—	28
D	—	—	—	1	—	—
Total	2,994	364	—	2	1	28

b) Subunit 26D, Sector IV

Guinea pig		Goat/Sheep		Goat/Sheep or Llama		Llama		Unknown	
Whole	Fragment	Whole	Fragment	Whole	Fragment	Whole	Fragment	Whole	Fragment
3,177	1,189	841	82	69	2	2,151	390	1,182	2,542

of the feces in the monumental part of Lo Demás probably has more to do with transportation of goods than with consumption of camelid meat (*see* Chapter 2 for a discussion of the ethnohistoric evidence for camelid presence and use in Chincha).

Work by Joyce Marcus (1987*a*, 1987*b*) in a nearby, Late Intermediate Period fishing site at Cerro Azul, Cañete, provides a useful comparison to the Lo Demás data. On excavating a large compound, Marcus found a room with llama dung covering the floor. Other rooms had contained large quantities of dried fish, and Marcus believes that the camelids were brought to the site to carry away dried fish as part of an exchange network with other segments of the Cañete valley and perhaps even with more distant groups. The fact that llama dung at Lo Demás was found in association with a rectangular compound similar to that excavated in Cerro Azul suggests a similar interpretation (*see* Chapters 11 and 12).

The Sector IV sample of animal coprolites presents one final problem, the presence of what appear to be sheep/goat feces. As mentioned above, sheep/goat and llama dung have a large overlap in size and form; the specimens identified as sheep/goat may actually be llama. Klausner found some specimens that fell squarely into the area of overlap; these are listed as "sheep/goat or llama" on Table 49b. However, there are still many examples which he felt were really sheep or goat. Most of these examples (71.2% of whole specimens, 23.1% of fragments, 67.0% overall in the goat/sheep category) occur between strata 26-1 and 26-3b, the levels identified on the basis of the molluscan and radiocarbon evidence as probably mixed; the lowest occurrence of apparent sheep/goat feces is in stratum 26-8. Sheep and goat were presumably present in Chincha by 1542, when the first Spanish monastery was founded there (*see* Chapter 2). These data support the other indications of mixing in the upper strata of Subunit 26D and the hypothesis that the Sector IV occupation lasted into the early Colonial Period.

IMPLICATIONS OF THE FAUNAL DATA FOR SPECIALIZATION

The faunal data offer several important pieces of information concerning specialization at Lo Demás. First, the overwhelming abundance of marine animals relative to terrestrial ones indicates that the inhabitants of the site had an intimate relationship with the sea, and that they relied on marine resources for the bulk of their meat. The patterning in the fish remains in terms of distribution by species and by skeletal element provides support for the notion that fish were processed at the site. However, the data also suggest that fish processing took place only in Sector I, and not in Sector IV. The Sector IV elite residents would have received processed fish for consumption and redistribution. Given the presence of camelid feces in the latter sector, it is likely that the elite residents were exporting some material, probably fish as tribute and for exchange.[108] Finally, the guinea pig remains from Sector I show that a *curandero*—a full- or part-time specialist—was operating at the site at least during the deposition of Complexes B and C.

CHAPTER 10

ORGANIC REMAINS: FLORA

This chapter reviews the data on flora from the excavations in Sectors I and IV of Lo Demás. Asunción Cano E. (Javier Prado Natural History Museum, Lima, Peru) identified the plant remains (Cano E., 1984, 1986*a*, 1986*b*, 1987). Descriptions of the various taxa from Lo Demás can be found in the published literature (Cohen, 1978; MacBride, 1936–1971; Towle, 1961). The sample studied by Cano E. includes the botanical remains retained in the ¼″ screen from the 1983 test excavations (Sector I), from Subunits 3B and 10D (Sector I), and from Subunit 26D (Sector IV), except certain plant parts that were considered as artifacts. These exceptions included the well-preserved gourd (*Lagenaria siceraria*) rind fragments, wooden objects, and cactus spine and wooden needles (*see* Chapter 8). As noted in Chapter 5, not all subunits contained all four stratigraphic complexes; the 1983 excavations lacked Complex B and Subunit 3B lacked Complex D. Subunit 26D was treated as a single stratigraphic complex. A total 12,247 specimens from Sector I[109] and 10,345 specimens from Sector IV were identified to the family, genus, or species level.

METHODOLOGY

The identification of the plant remains from Lo Demás involved several steps (Cano E., 1984:1). First, the material from each provenience was separated into like units according to the plant organ. Each of these groups was counted, and the condition of each specimen was noted (whole or fragment, burnt, gnawed, etc.). Next, the family, genus, and species of each group of like units was identified using published descriptions, photographs, and taxonomic keys. Finally, the results were checked against specimens in the Javier Prado Museum Herbarium and a field collection made in the vicinity of Lo Demás by Cano E. (1984, 1986*a*, 1987) on two visits. Each specimen was identified to the lowest possible taxonomic level; those specimens (mostly parts of stems) which could not be identified at least to the family level were not counted in the analysis. These unidentified specimens were saved for future analysis; it may be possible to identify them through microscopic inspection.

Using the identifications made by Cano E., I compiled the different proveniences into summary tables for each stratigraphic complex of Subunits 3B, 10D, and the 1983 test excavation. Subunit 26D was compiled into a single table. Organized by species, plant organ, and whether the specimen is whole or a fragment, these tables provided the database for the tables and analyses presented in the following sections of this chapter.

GENERAL CHARACTERISTICS OF THE LO DEMÁS BOTANICAL REMAINS

Table 50 provides a taxonomic chart of the plant remains identified from Lo Demás. The two best-represented families in terms of number of species are Leguminosae (legumes) and Gramineae (grasses). All of the identified taxa are native to the Peruvian coast except *Cynodon* cf. *dactylon,* an Old World introduction. Only one specimen of this species was recovered; its provenience is near the surface in Stratigraphic Complex D. The possible chronological implications of this specimen are discussed in Chapter 11.

The flora at Lo Demás comes from four major environmental zones: rocky shore, marsh/river bank, valley bottom, and *lomas* (seasonally fog-covered coastal hills) (*see* Table 51). All of these environments except the *lomas* (the least represented in terms of number of species and number of specimens) are found in the vicinity of Lo Demás (*see* Chapters 4 and 5). The valley bottom species can be further subdivided into cultigens grown in prepared fields, field invaders or weeds, and trees (probably cultivated). The greatest number of species and specimens are field cultigens, followed by species from humid, marshy habitats. In Chincha during the Late Horizon, the area between Lo Demás and the shoreline was marsh; the relative abundance of marsh plant specimens in the Lo Demás sample (1,835/22,592 = 8.1% by NISP [Number of Identified Specimens]) indicates that the fishermen of Chincha had access—probably direct—to the marsh zone, which would have been part of the fishermen's territory alluded to in the "Aviso" (Rostworowski, 1970:170) (*see* Chapter 2).

The potential uses of the plant species from Lo Demás fall into four major categories: food, industrial uses, medicine, and forage plants (Table 52). A review of the ethnobotanic literature indicates

Table 50.—*Taxonomic list of identified plant taxa from archaeological contexts at Lo Demás. Data from Cano E. (1984, 1986*a, *1986*b, *1987).*

- CRYPTOGAMAE
  - Chlorophytae
    - Ulvaceae
      - *Ulva* sp. (green algae)
  - Rhodophytae
    - Gigartinaceae
      - *Gigartina chamissoi* (C. Ag.) J. Ag. (red algae)
    - Phyllophoraceae
      - *Gymnogongrus* sp. (red algae)
- PHANEROGAMAE
  - Monocotyledonea
    - Typhaceae
      - *Typha angustifolia* L. (cattail)
    - Gramineae
      - *Phragmites australis* (Cav.) Trin. ex Steud. (reed grass)
      - *Gynerium sagittatum* (Aubl.) Beauv. ("caña brava")
      - *Cynodon* cf. *dactylon* (L.) Pers.
      - *Paspalum* sp.
      - *Cenchrus echinatus* L. (burr)
      - *Zea mays* L. (maize)
    - Cyperaceae
      - *Scirpus* cf. *californicus* (C. A. Mey.) Steud. ("totora")
    - Lemnaceae
      - *Lemna* sp. (duckweed)
    - Bromeliaceae
      - *Tillandsia* sp.
    - Cannaceae
      - *Canna edulis* Ker-Gawl ("achira")
  - Dicotyledonea
    - Salicaceae
      - *Salix* sp. (willow)
    - Leguminosae
      - *Inga feuillei* D. C. ("pacay")
      - *Caesalpina spinosa* (Mol.) Kuntze
      - *Pachyrrhizus* sp. ("jicama")
      - *Phaseolus lunatus* L. (lima bean)
      - *Phaseolus vulgaris* L. (common bean)
      - *Canavalia plagiosperma* Piper (jack bean)
      - *Arachis hypogaea* L. (peanut)
      - *Crotalaria incana* L.
    - Erythroxylaceae
      - *Erythroxylum* sp. (coca)
    - Malpighiaceae
      - *Bunchosia armeniaca* (Cav.) Rich. (monk's plum)
    - Malvaceae
      - *Gossypium barbadense* L. (cotton)
    - Myrtaceae
      - *Psidium guajaba* L. (guava)
    - Boraginaceae
      - *Heliotropium* sp.
    - Convolvulaceae
      - *Ipomoea batatas* (L.) Poir (sweet potato)
      - *Ipomoea* sp.
    - Verbenaceae
      - *Phyla nodiflora* (L.) Greene
    - Sapotaceae
      - *Pouteria lucuma* (R. & P.) O. Kuntze ("lucuma")

Table 50.—*Continued.*

- Solanaceae
  - *Nicandra physaloides* (L.) Gaertn.
  - *Physalis* sp.
  - *Capsicum frutescens* L. (ají pepper)
- Cucurbitaceae
  - *Cucurbita maxima* Duch. (squash)
  - *Cucurbita pepo* (squash)
  - *Cucurbita* sp.
  - *Lagenaria siceraria* (Mol.) Standl. (gourd)

that only three of the identified taxa have no previously suggested prehistoric uses: *Gymnogongrus* sp. (red algae), *Lemna* sp. (duckweed), and *Nicandra physaloides.* According to Sagástegui (1973), *Nicandra physaloides* is toxic to man and animal, and it may have had some medicinal or shamanic role. *Gymnogongrus* is currently important in the production of agar for culturing bacteria (Acleto, 1971).

Of the plants listed as potential food sources, the predominant kinds of organs recovered from the archaeological contexts tend to accord with food use. Some of the remains are the actual edible portion, but more frequently encountered were elements which come as a "package" with the edible portion. For instance, maize (*Zea mays*) cobs were quite abundant (264 whole, 1,891 fragments), as were lucuma (*Pouteria lucuma*) testa (seed coats from the pits of the fruit) and seeds (24 whole testa, 2,162 testa fragments; 9 whole seeds, 56 seed fragments) and peanut (*Arachis hypogaea*) shells (20 whole, 2,427 fragments).

Roots and tubers present a greater problem, as the edible portion is totally consumable and often is not transported in association with inedible elements. Three of the edible root plants identified in the Lo Demás remains are cultigens (*Canna, Pachyrrhizus,* and *Ipomoea*). Few specimens of these species were found among the botanical remains from Lo Demás. Of the five sweet potato (*Ipomoea batatas, Ipomoea* sp.) elements, four were whole or fragmented tuberous roots, while the seven achira (*Canna edulis*) fragments included one piece of a rhizome. In contrast, the 70 identified jicama (*Pachyrrhizus* sp.) specimens included fruits, pericarp fragments and seeds, but no tubers. It seems clear that sweet potatoes and achira were consumed, though reliable estimates of their dietary importance are not possible. The jicama case is more ambiguous; Towle (1961:51–52) notes that *Pachyrrhizus* seeds are toxic. Rostworowski (1970:170) mentions

Table 51.—*Plant taxa from Lo Demás by habitat. Compiled from Cano E. (1984, 1986*a*, 1986*b*, 1987) and Towle (1961).* [a] *According to Cano E. (1984:6),* Salix *grows in humid or swampy ground and along the edge of irrigation canals, but is also planted around the edges of fields as a living fence.* [b] *According to Towle (1961: 4),* Caesalpina spinosa *grows wild along river banks in the lomas zone, but is also planted.*

Rocky Shore

Ulva sp.
Gigartina chamissoi
Gymnogongrus sp.

Marsh/River Banks

Scirpus cf. *californicus*
Gynerium sagittatum
Paspalum sp.
Phragmites australis
Lemna sp.
Typha angustifolia
Salix sp.[a]

Field Cultigens

Canna edulis
Cynodon cf. *dactylon*
Zea mays
Ipomoea batatas
Cucurbita maxima
Cucurbita pepo
Lagenaria siceraria
Arachis hypogaea
Canavalia plagiosperma
Pachyrhizus sp.
Phaseolus lunatus
Phaseolus vulgaris
Gossypium barbadens
Capsicum frutescens

Field Invaders (Weeds)

Cenchrus echinatus
Heliotropium sp.
Crotalaria incana
Nicandra physaloides
Physalis sp.
Phyla nodiflora

Valley (Trees and Shrubs)

Inga feuillei
Bunchosia armeniaca
Psidium guajaba
Salix sp.[a]
Pouteria lucuma
Erythroxylum sp.

Lomas

Tillandsia sp.
Caesalpina spinosa[b]

"the planting of ... seeds and roots" by the valley's farmers.

The two other plants with edible tubers are the marsh reeds *Typha angustifolia* and *Scirpus* cf. *californicus.* The remains of both species are dominated by aerial elements, mainly stems and leaves. However, three rhizome fragments of *Typha angustifolia* were included in the botanical sample from Lo Demás. Although one or both of these plants were probably consumed at the site, their more important use was as a source of construction material for matting (pieces of reed mats were encountered in the deposits—*see* Chapter 6) and perhaps for reed rafts (the "Aviso" says that each fisherman went to sea on a raft [Rostworowski, 1970:170]). The large number of stem fragments of these species found in the archaeological deposits supports this interpretation.

Table 52.—*Plant taxa from Lo Demás by potential use. Compiled from uses cited by Cano E. (1984, 1986*a*, 1986*b*, 1987), Morton (1981), and Towle (1961). Species for which the potential use is indicated or strongly supported at Lo Demás are marked with an asterisk. A question mark indicates some doubt concerning the identification of specimens to the indicated taxonomic level.*

Food

Algae: *Ulva* sp.*, *Gigartina chamissoi**
Grains: *Zea mays**
Legumes: *Arachis hypogaea**, *Canavalia plagiosperma**, *Inga feuillei**, *Phaseolus lunatus**, *Phaseolus vulgaris**
Condiments: *Capsicum frutescens**
Beverages: *Zea mays*
Fruits: *Cucurbita maxima**, *Cucurbita pepo**, *Lagenaria siceraria**, *Bunchosia armeniaca**, *Psidium guajaba**, *Pouteria lucuma**, *Physalis* sp.*
Roots and tubers: *Canna edulis**, *Ipomoea batatas**, *Pachyrhizus* sp., *Scirpus* cf. *californicus, Typha angustifolia**

Industrial

Dyes and tannins: *Caesalpina spinosa*
Fruits for utensils: *Lagenaria siceraria**
Fibers and stems: *Tillandsia* sp., *Canna edulis, Scirpus* cf. *californicus**, *Gynerium sagittatum**, *Phragmites australis**, *Zea mays, Typha angustifolia**, *Gossypium barbadense**
Woods: *Gynerium sagittatum**, *Inga feuillei, Salix* sp.
Living fence: *Salix* sp.
Reed rafts: *Scirpus* cf. *californicus*?, *Typha angustifolia*?

Medicine

Canna edulis
Cynodon cf. *dactylon*
Tillandsia sp.
Gynerium sagittatum
Paspalum sp.
Zea mays
Heliotropium sp.
Ipomoea batatas
Cucurbita maxima
Lagenaria siceraria
Erythroxylum sp.
Crotalaria incana
Pachyrhizus sp.
Caesalpina spinosa
Gossypium barbadense
Psidium guajaba
Salix sp.
Pouteria lucuma
Capsicum frutescens
Physalis sp.
Phyla nodiflora

Forage

Cynodon cf. *dactylon*
Paspalum sp.

Of the other industrial plants, there is clear evidence for use of cotton (*Gossypium barbadense*) for nets and thread (*see* Chapter 8). Canes of either *Gynerium* or *Phragmites* were found in situ in channels in Sector I, where they formed part of a *quincha* structure in Stratigraphic Complex D (*see* Chapter 6). Fragments of gourd rind (pericarp) (*Lagenaria siceraria*) were found throughout the deposit, many with cut edges and several with pyroengraved designs (*see* Chapter 8), attesting to the use of gourds as containers or utensils. Later in this chapter, I discuss in detail the evidence for gourd utensil pro-

Table 53.—*Number of identified plant specimens (NISP), percent, and rank by taxon and stratigraphic complex from 1983 test excavations, Sector I. Complex A is not included* (see *note 109). A question mark indicates some doubt concerning the identification of specimens to the indicated taxonomic level.*

Species	Complex C			Complex D		
	NISP	%	Rank	NISP	%	Rank
Ulva sp.	—	—	—	1	—	35
Gigartina chamissoi	6	0.3	23	29	0.6	15
Gymnogongrus sp.	26	1.3	12	1	—	35
Typha angustifolia	—	—	—	227	5.1	4
Typha sp.	4	0.2	27	—	—	—
Typha?	8	0.4	18	3	0.1	30
Liliaceae or Amarylladaceae?	7	0.4	20	—	—	—
Gramineae	120	6.0	6	114	2.5	7
Phragmites australis	8	0.4	18	—	—	—
Phragmites sp.	6	0.3	23	27	0.6	18
Phragmites?	13	0.7	17	16	0.4	25
Gynerium or *Phragmites*	4	0.2	27	27	0.6	18
Gynerium sagittatum	16	0.8	15	—	—	—
Cynodon dactylon	—	—	—	1	—	35
Paspalum sp.	—	—	—	1	—	35
Cenchrus echinatus	145	7.3	4	124	2.8	6
Zea mays	619	31.1	1	2,025	45.3	1
Cyperaceae?	90	4.5	8	81	1.8	8
Scirpus cf. *californicus*	7	0.4	20	57	1.3	12
Scirpus?	—	—	—	28	0.6	17
Tillandsia sp.	7	0.4	20	10	0.2	27
Canna edulis?	1	0.1	29	—	—	—
Amaranthaceae?	—	—	—	7	0.2	28
Cactaceae?	—	—	—	1	—	35
Salix sp.	1	0.1	29	2	—	32
Leguminosae	12	0.6	18	24	0.5	21
Inga feuillei	5	0.3	25	2	—	32
Inga?	—	—	—	1	—	35
Caesalpina spinosa?	5	0.3	25	—	—	—
Pachyrhizus sp.	—	—	—	66	1.5	11
Phaseolus lunatus	19	1.0	14	46	1.0	13
Phaseolus vulgaris	31	1.6	11	21	0.5	23
Phaseolus sp.	—	—	—	21	0.5	23
Phaseolus?	1	0.1	29	22	0.5	22
Canavalia plagiosperma	—	—	—	39	0.9	14
Canavalia?	—	—	—	1	—	35
Arachis hypogaea	188	9.5	3	168	3.8	5
Crotalaria incana	33	1.7	10	2	—	32
Bunchosia armeniaca	1	0.1	29	—	—	—
Gossypium barbadense	109	5.5	7	451	10.1	3
Ipomoea batatas	—	—	—	1	—	35
Ipomoea sp.	—	—	—	1	—	35
Verbenaceae?	—	—	—	1	—	35
Pouteria lucuma	258	13.0	2	598	13.4	2
Capsicum frutescens	127	6.4	5	29	0.6	15
Capsicum?	1	0.1	29	3	0.1	30
Cucurbitaceae?	—	—	—	7	0.2	28
Cucurbita sp.	73	3.7	9	67	1.5	10
Cucurbita?	14	0.7	16	81	1.8	8
Lagenaria siceraria	23	1.2	13	26	0.6	20
Lagenaria?	1	0.1	29	15	0.3	26
Total	1,989			4,473		

Table 54.—*Number of identified plant specimens (NISP), percent, and rank by taxon and stratigraphic complex from Subunit 3B, Sector I. Complex A is not included* (see *note 109). A question mark indicates some doubt concerning the identification of specimens to the indicated taxonomic level.*

Species	Complex B			Complex C		
	NISP	%	Rank	NISP	%	Rank
Gigartina chamissoi	—	—	—	5	0.2	19
Gymnogongrus?	—	—	—	10	0.4	16
Typha sp.	15	1.7	13	3	0.1	21
Gramineae	—	—	—	116	5.2	6
Phragmites australis	27	3.1	9	40	1.8	12
Gynerium sagittatum	—	—	—	24	1.1	15
Paspalum sp.	—	—	—	2	0.1	25
Cenchrus echinatus	58	6.6	6	60	2.7	10
Zea mays	257	29.4	1	530	23.8	1
Cyperaceae	—	—	—	4	0.2	20
Scirpus cf. *californicus*	69	7.9	5	152	6.8	5
Scirpus sp.	14	1.6	14	363	16.3	2
Tillandsia sp.	—	—	—	1	—	28
Canna sp.	—	—	—	6	0.3	18
Leguminosae	—	—	—	38	1.7	13
Inga feuillei	4	0.5	15	3	0.1	21
Pachyrhizus sp.	2	0.2	16	2	0.1	25
Phaseolus lunatus	1	0.1	17	8	0.4	17
Phaseolus vulgaris	16	1.8	11	66	3.0	9
Phaseolus sp.	—	—	—	1	—	28
Canavalia sp.	16	1.8	11	—	—	—
Canavalia?	—	—	—	1	—	28
Arachis hypogaea	109	12.5	2	79	3.5	8
Crotalaria sp.	—	—	—	3	0.1	21
Bunchosia armeniaca	1	0.1	17	1	—	28
Gossypium barbadense	38	4.3	7	115	5.2	7
Heliotropium sp.	1	0.1	17	2	0.1	25
Pouteria lucuma	72	8.2	4	267	12.0	3
Nicandra physaloides	—	—	—	3	0.1	21
Physalis sp.	1	0.1	17	—	—	—
Capsicum frutescens	38	4.3	7	31	1.4	14
Cucurbita maxima	—	—	—	1	—	28
Cucurbita sp.	109	12.5	2	239	10.7	4
Lagenaria siceraria	25	2.9	10	50	2.2	11
Total	874			2,226		

duction in Sector IV. Several large wooden artifacts are described in Chapter 8, as are wood and cactus spine needles; these artifacts were not enumerated in the botanical samples because they could not be securely identified. There is no direct evidence for the other industrial uses listed in Table 52.

The distribution of potential medicinal species between Sectors I and IV at Lo Demás suggests localization of activities carried out at the site. Only 12 of the 21 species for which medicinal use is known are present in Sector IV, while 19 are present in Sector I (cf. Table 52 with Tables 53–56).[110] However, one of the medicinal species found in Sector I (*Cynodon* cf. *dactylon*) is a postconquest introduction in the Andes and may be intrusive at Lo Demás. Although sample size effect probably accounts for some of the difference between sectors,[111] the condition of the guinea pig remains in Sector I (*see* Chapter 9) suggests that the difference is due to the operation of a *curandero* in Sector I. In this context, it is interesting to note that the stomach contents of one of the burials in Sector II, an adult between 20 and 25 years of age (G. Elera N., personal communication, 1984), contained a large quantity of *Capsicum* seeds and Dicotyledoneae fibers from masticated twigs (Jones, 1986). Three quarters of the medicinal plants from Lo Demás are dicots, including the three taxa known only for me-

Table 55.—*Number of identified plant specimens (NISP), percent, and rank by taxon and stratigraphic complex from Subunit 10D, Sector I. Complex A is not included* (see *note 109). A question mark indicates some doubt concerning the identification of specimens to the indicated taxonomic level.*

Species	Complex B			Complex C			Complex D		
	NISP	%	Rank	NISP	%	Rank	NISP	%	Rank
Ulva sp.	—	—	—	—	—	—	6	1.1	12
Gigartina chamissoi	—	—	—	4	0.6	13	6	1.1	12
Gymnogongrus?	—	—	—	—	—	—	15	2.8	10
Gramineae	90	6.1	4	10	1.5	10	2	0.4	16
Phragmites australis	13	0.9	10	13	1.9	9	1	0.2	20
Phragmites sp.	4	0.3	14	3	0.4	14	37	7.0	6
Gynerium sagittatum	3	0.2	15	2	0.3	15	3	0.6	15
Cenchrus echinatus	50	3.4	5	6	0.9	12	2	0.4	16
Zea mays	441	29.9	2	148	21.7	2	83	15.7	2
Scirpus cf. *californicus*	—	—	—	1	0.1	16	50	9.5	4
Scirpus?	—	—	—	1	0.1	16	—	—	—
Lemna sp.	—	—	—	40	5.9	5	25	4.7	8
Tillandsia sp.	—	—	—	—	—	—	2	0.4	16
Leguminosae	15	1.0	9	—	—	—	—	—	—
Inga feuillei	43	2.9	6	111	16.3	4	103	19.5	1
Phaseolus lunatus?	1	0.1	18	—	—	—	—	—	—
Phaseolus vulgaris	—	—	—	—	—	—	25	4.7	8
Canavalia?	2	0.1	17	—	—	—	—	—	—
Arachis hypogaea	591	40.1	1	125	18.3	3	43	8.1	5
Crotalaria sp.	6	0.4	12	—	—	—	2	0.4	16
Bunchosia armeniaca	1	0.1	18	—	—	—	—	—	—
Gossypium barbadense	28	1.9	8	14	2.1	8	10	1.9	11
Psidium guajaba?	1	0.1	18	—	—	—	—	—	—
Labiatae	10	0.7	11	—	—	—	—	—	—
Pouteria lucuma	131	8.9	3	156	22.9	1	71	13.4	3
Capsicum frutescens	5	0.3	13	—	—	—	—	—	—
Cucurbita sp.	36	2.4	7	19	2.8	7	—	—	—
Cucurbita?	—	—	—	21	3.1	6	37	7.0	6
Lagenaria siceraria	3	0.2	15	8	1.2	11	5	0.9	14
Compositae	1	0.1	18	—	—	—	—	—	—
Total	1,475			682			528		

dicinal use. Analysis of pollen from the Burial II stomach contents found only 19 pollen grains: two were *Tillandsia* sp. (a plant with medicinal uses recovered archaeologically in Sectors I and IV), ten were *Haageocereus* sp. (a columnar cactus), and the rest could not be identified at the genus level (Jones, 1986).

The two species listed under the category of forage are very poorly represented in the botanical sample from Lo Demás (only four specimens), and one of the species (*Cynodon* cf. *dactylon*)—represented by a single specimen—is a possibly intrusive Old World plant. However, the guinea pigs kept at the site could have eaten parts of other plants found in the sample, particularly the maize leaves and stalks. These maize by-products are still used to feed guinea pigs in Peru (Bolton and Calvin, 1981:281–283). A planned study of phytoliths and other botanical elements from Lo Demás guinea pig feces will help determine which of the plant remains at the site contributed to the rodents' diet.

Quantitative Analysis

Limitations

Quantitative analysis of the Lo Demás plant remains presents two kinds of limitations: those inherent in archaeobotanical studies in general, even in an environment as apparently ideal as the desert coast of Peru (*see* Cohen, 1972–1974), and those resulting from the nature of the Lo Demás sample.

Cohen (1972–1974) points out several problems. Both differential use and differential preservation of plant parts can bias the archaeological record. If only

Table 56.—*Number of identified plant specimens (NISP), percent, and rank by taxon from Subunit 26D, Sector IV. A question mark indicates some doubt concerning the identification of specimens to the indicated taxonomic level.*

Species	NISP	%	Rank
Gigartina chamissoi	481	4.6	7
Gymnogongrus?	14	0.1	26
Typha sp.	7	—	27
Gramineae	55	0.5	17
Phragmites australis	87	0.8	14
Phragmites sp.	1	—	33
Gynerium or *Phragmites*	5	—	29
Gynerium sagittatum	187	1.8	11
Cenchrus echinatus	347	3.4	9
Zea mays	1,834	17.7	2
Cyperaceae	45	0.4	21
Scirpus cf. *californicus*	17	0.2	22
Scirpus sp.	92	0.9	13
Lemna sp.	70	0.7	15
Tillandsia sp.	51	0.5	19
Leguminosae	107	1.0	12
Inga feuillei	57	0.6	16
Phaseolus lunatus	6	—	28
Phaseolus vulgaris	49	0.5	20
Phaseolus sp.	53	0.5	18
Canavalia sp.	5	—	29
Arachis hypogaea	1,041	10.1	4
Crotalaria sp.	1	—	33
Erythroxylum sp.	16	0.2	23
Bunchosia armeniaca	16	0.2	23
Gossypium barbadense	2,180	21.1	1
Psidium guajaba	1	—	33
Ipomoea batatas	3	—	31
Phyla nodiflora	2	—	32
Pouteria lucuma	673	6.5	6
Capsicum frutescens	452	4.4	8
Capsicum sp.	210	2.0	10
Cucurbita pepo	16	0.2	23
Cucurbita sp.	985	9.5	5
Lagenaria siceraria	1,179	11.4	3
Total	10,345		

the edible portions of certain plants are brought to a given location, few remains from those species will be found in the archaeological deposits relative to the actual numbers consumed. The tubers discussed above are a case in point. Similarly, if only easily decayed parts of particular species are brought to a site, those species will not be present or will be underrepresented in the record. Therefore, there is a bias towards recovery of plant taxa which have a utilized portion that is itself, or is generally associated with, a decay-resistant plant organ.

A second set of problems raised by Cohen (1972–1974) involves the nature of plant taxonomy. First, most plants are differentiated taxonomically by their flowering parts, but these parts are rarely the economically useful organs and even more rarely are they preserved. Second, botanists tend to concentrate on plants of current economic importance; thus, many species utilized prehistorically are poorly known. These two conditions probably result in biases in terms of the identified portion of preserved plant remains—"wild plants and ones of little contemporary importance . . . will almost always be underrepresented in the *identified* refuse" (Cohen, 1972–1984:55). However, the Lo Demás plant identifications are based on a local (Chincha valley) type collection and the extensive Peruvian herbarium at the Javier Prado Natural History Museum, mitigating the potential identification bias.

Finally, Cohen (1972–1974:52) notes an empirical problem arising from his studies of plant remains from the central coast of Peru. Although the same *range* of taxa is found in sites of differing age, there appears to be a significant difference in the overall *quantity* of preserved specimens between the Late Horizon and all previous periods, with plant remains much more abundant in the Late Horizon. Cohen does not see important environmental differences between the sites in his sample, and he considers the abruptness of the change (from the Late Intermediate Period to the Late Horizon) too fast to be accounted for by differential decay along a temporal continuum. Cohen concludes that only cultural factors can explain this phenomenon, though he does not suggest what these factors might be. However, because Lo Demás is a Late Horizon site, the decrease in recovered remains noted for earlier sites does not apply.

While the problems raised by Cohen are important, they do not affect seriously the kinds of analyses undertaken in this chapter. Cohen's principal concern, quantitative reconstruction of vegetable diet, is not attempted here. The general discussion of the Lo Demás plant remains in the preceding section dealt primarily with presence/absence rather than quantitative criteria. The analyses presented in the following sections are concerned mainly with variation in the relative frequencies of identified specimens from Lo Demás. Systematically absent, decayed, or unidentified taxa are therefore of little importance. I have made several assumptions, however. Because the occupation of the excavated component of Lo Demás was quite short and falls wholly within the Late Horizon, I assume that differential decay between stratigraphic complexes has not biased the sample. From this assumption, and given

Table 57.—*Total number of identified plant specimens (NISP), percent, and rank by taxon (genus or species) and stratigraphic complex for Sector I of Lo Demás. Complex A is not included* (see *note 109). Complex B combines Subunits 3B and 10D. Complex C combines Subunits 3B and 10D with all four 1983 subunits. Complex D combines Subunit 10D with the 1983 subunits. Percentages are calculated on the total number of identified specimens for each stratigraphic complex* (see *Tables 53–55). Only those species with an overall frequency of greater than 2% are included in this table (cf. Tables 53–55). Material not securely identified at least to genus level is not included.*

	Complex B			Complex C			Complex D		
Species	NISP	%	Rank	NISP	%	Rank	NISP	%	Rank
Typha angustifolia	—	—	—	—	—	—	227	4.5	4
Cenchrus echinatus	108	4.6	5	211	4.3	7	126	2.5	6
Zea mays	690	29.7	2	1,297	26.5	1	2,108	42.2	1
Scirpus cf. *californicus*	69	2.9	6	160	3.3	8	107	2.1	7
Scirpus sp.	—	—	—	363	7.4	4	—	—	—
Inga feuillei	47	2.0	8	119	2.4	10	105	2.1	8
Phaseolus vulgaris	—	—	—	97	2.0	11	—	—	—
Arachis hypogaea	700	29.8	1	392	8.0	3	211	4.2	5
Gossypium barbadense	66	2.8	7	238	4.9	6	461	9.2	3
Pouteria lucuma	203	8.6	3	681	13.9	2	669	13.4	2
Capsicum frutescens	—	—	—	158	3.2	9	—	—	—
Cucurbita sp.	145	6.2	4	331	6.8	5	—	—	—
Total this table	2,028	86.3		4,047	82.6		4,014	80.3	
Complex total	2,349			4,897			5,001		

the standardized recovery procedure (¼″ screen), it follows that observed variations in the number and kind of identified specimens per taxon should represent real differences in activities carried out at the loci of excavation.

However, there is one further limitation of the data: the size and distribution of the sample of identified plant specimens from Lo Demás. Almost as many specimens were identified from Sector IV (10,345)[112] as from Sector I (12,247), but the volume of the studied deposits is much greater in Sector I (*see* note 111). Because Sector I and Sector IV are contemporaneous, this difference in density should represent a difference in the kind or intensity of activities carried out at the two excavation areas. However, it is likely that the proximity of each sample to the foci of activities and perhaps post-depositional history also account for some of the differences in density of remains. Thus, the two samples may not be equally representative of their respective sectors. Tables 53–55 indicate the number of identified plant specimens (whole plus fragments) by stratigraphic complex for the 1983 excavations (pooled), Subunit 3B, and Subunit 10D in Sector I. Table 56 provides the same data for Subunit 26D in Sector IV. The subunit samples of the Sector I plant remains show some variation in composition by complex. Although it is unclear to what degree these variations reflect different activity loci and to what degree they represent random variation, comparison of the frequencies of common taxa between different members of the same complex in Sector I shows broad agreement and provides a basis for careful interpretation.

Analysis by Stratigraphic Complex in Sector I

For this analysis, the different members of each stratigraphic complex in Sector I have been pooled into complex totals to see changes through time in the importance of predominant plant taxa (Table 57) and organs (Table 58).

Table 57 shows an increase in maize (*Zea mays*) following Complex C and a decrease in peanut (*Arachis hypogaea*) following Complex B. In Complex C, these changes are associated with increased leaf specimens (maize leaves dominate this category) and decreased pericarp specimens (*Arachis* pericarps—peanut shells—predominate in this category) (Table 58). The increase in testa following Complex B is also to be expected; it parallels the general increase in lucuma (*Pouteria lucuma*) specimens, which dominate the testa category. Less predictable from the distribution by species is the increase in stem fragments in Complex C as compared with either the preceding or succeeding complexes.

The differences between Complex B and the succeeding complexes may result in part from different modes of deposition; Complex B consists of refuse thrown outside the living areas to the west of the Sector I excavations, while Complexes C and D are

Table 58.—*Total number of identified plant specimens (NISP), percent, and rank by plant organ and stratigraphic complex for Sector I of Lo Demás. Complex A is not included* (see *note 109). Complex B combines Subunits 3B and 10D. Complex C combines Subunits 3B and 10D with all four 1983 subunits. Complex D combines Subunit 10D with the 1983 subunits. Percentages are calculated on the total number of identified specimens for each stratigraphic complex* (see *Tables 53–55). Only those organs with an overall frequency of greater than 2% are included in this table (cf. Tables 53–55). All material identified to family level is included.*

Organ	Complex B			Complex C			Complex D		
	NISP	%	Rank	NISP	%	Rank	NISP	%	Rank
stem	341	14.5	2	1,262	25.8	1	661	13.2	5
cane	—	—	—	122	2.5	8	—	—	—
leaf	57	2.4	6	392	8.0	6	1,064	21.3	1
fruit	136	5.8	5	377	7.7	7	479	9.6	8
pericarp	765	32.5	1	607	12.4	3	356	7.1	7
seed	259	11.0	3	573	11.7	4	612	12.2	6
testa	204	8.7	4	827	16.9	2	790	15.8	2
cob	494	21.0	2	424	8.7	5	707	14.1	3
seed coat	—	—	—	121	2.5	8	—	—	—
Total this table	2,256	96.0		4,705	96.1		4,669	93.4	
Complex total	2,349			4,897			5,001		

midden deposits in direct association with a sequence of floors (*see* Chapter 5). However, Complex B does not differ from the other complexes in all categories. The proportion of maize stays constant from Complex B to Complex C and only changes in Complex D. The proportions of stem fragments in Complexes B and D are nearly the same; only Complex C differs. These patterns suggest that Complex B can be compared with the other two complexes.

The differences between complexes suggest several interpretations concerning changes in activities through time in Sector I. The shift from peanut to maize as the major food species represented by the plant sample may indicate a change in the pattern of plant food acquisition by the inhabitants of Sector I. The increase in maize specimens may be related to a greater degree of interaction with other groups in Chincha. Although maize specimens do not increase in absolute frequency until Complex D, they triple in relation to peanut fragments from Complex B to Complex C (Table 57) (maize specimens are ten times more frequent than peanut specimens in Complex D), placing the beginning of the peanut/maize shift at the same time as the increase in stem fragments. Almost 50% of the stem fragments from Complex C are from members of the Cyperaceae family, which is the taxon used to make reed boats and rafts. Complex C may witness an increase in fishing by the inhabitants of Sector I of Lo Demás, with a concomitant increase in acquisition of goods (maize) exchanged for fish with local farmers and other specialists. This suggestion is discussed further in Chapter 12 in the context of other classes of data.

Analysis by Sector

For analysis by sector, the total of identified plant specimens from Complexes B to D in Sector I was compared with the Sector IV total. Comparisons between Sector IV and individual complexes from Sector I were not attempted because Subunit 26D probably spans all three complexes but cannot be securely subdivided into equivalent units.

The variations in frequency of identified plant specimens both by species and by organ are large enough to suggest real differences between the areas. In terms of species (Table 59), the most striking contrast is in the relative importance of cotton (*Gossypium barbadense*), which predominates in Sector IV, and maize (*Zea mays*), which predominates in Sector I. This contrast is associated with a major difference in the importance of seeds among the recovered plant organs (Table 60); seeds and seed fragments accounted for nearly half of the identified specimens in Sector IV, over three times as frequent as in Sector I. In Sector IV, the seed category was dominated primarily by cotton and secondarily by gourd (*Lagenaria siceraria*) and squash (*Cucurbita* sp.), while in Sector I, cotton and squash seed specimens were about equal and gourd remains of any kind were scarce. This fact highlights the second major contrast between the samples from Sectors I and IV: the importance of gourd specimens (*Lag-*

Table 59.—*Total number of identified plant specimens (NISP), percent, and rank by taxon and sector of Lo Demás. For Sector I, Complex A is not included* (see *note 109). Percentages are calculated on the total number of identified specimens in Complexes B–D in Sector I and for the Subunit 26D total for Sector IV* (see *Tables 53–56). Only those species with an overall frequency of greater than 2% are included in this table (cf. Tables 53–56). Material not securely identified at least to genus level is not included.*

Species	Sector I			Sector IV		
	NISP	%	Rank	NISP	%	Rank
Gigartina chamissoi	—	—	—	481	4.6	7
Cenchrus echinatus	445	3.6	6	347	3.4	9
Zea mays	4,095	33.4	1	1,834	17.7	2
Scirpus cf. *californicus*	336	2.7	8	—	—	—
Scirpus sp.	377	3.1	7	—	—	—
Inga feuillei	271	2.2	0	—	—	—
Arachis hypogaea	1,303	10.6	3	1,041	10.1	4
Gossypium barbadense	765	6.2	4	2,180	21.1	1
Pouteria lucuma	1,553	12.7	2	673	6.5	6
Capsicum frutescens	—	—	—	452	4.4	8
Capsicum sp.	—	—	—	210	2.0	10
Cucurbita sp.	543	4.4	5	985	9.5	5
Lagenaria siceraria	—	—	—	1,179	11.4	3
Total this table	9,688	79.1		9,382	90.7	
Sector total	12,247			10,345		

enaria siceraria) in Sector IV and their minimal recovery from Sector I.

The third important difference between sectors is the presence of coca (*Erythroxylum* sp.) in Sector IV and its absence in Sector I. As today, coca was used in pre-Hispanic times as a medicinal plant and "as a mild stimulant and as sustenance for working under harsh environmental conditions" (Plowman, 1986:5). It was also important "for offerings, ceremonies to the *huacas*, curing rituals, and divination" (Rostworowski, 1988*b*:64). Murra (1986) has recently argued that access to coca in the Andean world was not restricted to elites, but instead available to all. However, the Inka reorganized coca production throughout much of their empire (Netherly, 1988*b*), and it is likely that access to coca came under greater control in the Late Horizon. In any case, the distribution of coca remains at Lo Demás argues for differential access to this plant.

The last notable difference between the two sectors is the abundance (nearly 5%) of algal thalli (mostly *Gigartina chamissoi*) in the Sector IV sample and the virtual absence of algae in the Sector I sample. Algae may have been used to pack fish or

Table 60.—*Total number of identified plant specimens (NISP), percent, and rank by plant organ and sector of Lo Demás. For Sector I, Complex A is not included* (see *note 109). Percentages are calculated on the total number of identified specimens in Complexes B–D in Sector I and for the Subunit 26D total for Sector IV* (see *Tables 53–56). Only those organs with an overall frequency of greater than 2% are included in this table (cf. Tables 53–56). All material identified at least to family level is included.*

Organ	Sector I			Sector IV		
	NISP	%	Rank	NISP	%	Rank
thallus	—	—	—	495	4.8	7
stem	1,669	13.6	3	1,056	10.2	3
leaf	1,513	12.4	5	393	3.8	8
fruit	992	8.1	7	771	7.5	4
pericarp	1,728	14.1	2	1,120	10.8	2
seed	1,444	11.8	6	4,702	45.5	1
testa	1,821	14.9	1	645	6.2	5
cob	1,625	13.3	4	505	4.9	6
Total this table	10,792	88.1		9,687	93.6	
Sector total	12,247			10,345		

shellfish for transportation, or may itself have been a trade or tribute item, as it has been since the Spanish conquest (Masuda, 1981, 1982).

Subunit 26D, the source of the Sector IV sample, lies next to Building IV–2, a large, rectangular enclosure, and consists mainly of refuse thrown out of that building (*see* Chapter 5). The remains from 26D should therefore relate to activities carried out in the enclosure. The predominance of an industrial plant (cotton) in Subunit 26D suggests that productive activities involving fiber processing were more important in Building IV–2 than in the residential area in Sector I. Building IV–2 at Lo Demás is built of the large, rectangular *adobes* associated with Inka-related structures in Chincha (*see* Chapters 4 and 6); Craig Morris (1985) found evidence of textile manufacture in the Inka precinct at nearby La Centinela.

Cotton was certainly important in Sector I, as well; the presence of seeds, fiber, and other *Gossypium* organs in the Sector I sample together with net fragments, a net making tool, a wooden weaving tool, spinning equipment, needles, threads, and patched pieces of cotton cloth (*see* Chapter 8) indicate that cotton thread was spun, employed in net manufacture and repair, and used for patching torn and worn out cloth. Indeed, the only direct evidence for the use of the cotton in Sector IV consisted of nine needle fragments, three spindle fragments, four whole or broken spindle whorls, a bone weaving tool, and a possible bone *mallero,* all from Subunit 26D (*see* Chapter 8). Nevertheless, the great abundance of cotton remains in Sector IV attests to the importance of fiber processing in that sector.

The importance of gourd in Sector IV is also related to productive activities taking place in Building IV–2. The *Lagenaria siceraria* specimens from the Subunit 26D *botanical* sample consist entirely of seeds and seed fragments (1,179 specimens—*see* Table 56). As artifacts, the well-preserved gourd pericarp (rind) fragments from the Lo Demás excavations were treated separately from the botanical sample (*see* Chapter 8). In Subunit 26D, 255 such fragments were recovered, including six rim sherds, 17 other examples with cut marks, six pieces with incised or pyroengraved decoration, and 33 peduncles (13% of total gourd rind fragments; *see* Chapter 8, Table 13). Peduncles are the point where the stem connects to the gourd. Peduncles and seeds are removed in preparing gourds for use as utensils. Far fewer pericarp fragments were found in Sector I—for instance, only 59 were recovered from Subunit 10D—and peduncles were quite rare (only three—5% of the total—were found; *see* Chapter 8, Table 12). These data strongly suggest that production of gourd utensils was carried out in Building IV–2, but not in the excavated area of Sector I. According to Rostworowski (1970:156–157), gourd containers were one of the local products carried as trade items by the merchants of Chincha, and gourds were found in many of the graves excavated by Uhle (Kroeber and Strong, 1924:36–37; Whitaker, 1948:54–55).

In accordance with ethnohistoric data for the coast (*see* Chapter 2), the group of monumental structures in Sector IV would have housed a Chincha local level lord, probably a lord of fishermen. Among the structures in this precinct, Building IV–2 and the activities it housed must have had a high status, given both the original size of the structure and the use of Inka-related rectangular *adobes.* Considering the abundance of industrial plant specimens in the Sector IV botanical sample, Building IV–2 may have housed artisans attached to the lord. Such a situation is known from ethnohistoric documents for the north coast (Hart, 1983:254–255; also Rostworowski, 1977, 1981; Netherly, 1977; Ramirez-Horton, 1982) and is parallelled to a degree in the archaeological evidence for artisan production at Chan Chan, the Late Intermediate Period Chimu capital in the north coast Moche valley (Topic, 1982). Among the ethnohistorically documented obligations of Andean lords, both the provision of food and drink and the presentation of textiles were of extreme importance (Murra, 1980). At the highland Inka administrative center of Huanuco Pampa, Morris and Thompson (1985) found abundant ceramic evidence for the production and consumption of chicha (maize beer) and food associated with the high status sector of the site. On the coast, gourds may well have replaced the ceramic serving vessels used in the highlands. It is therefore possible that the gourd utensils and cotton products manufactured in Building IV–2 were for the use of the local lord presiding over Sector IV of Lo Demás, and not for trade by the merchants. This topic is discussed further in Chapters 11 and 12. In either case, the gourd remains provide clear evidence of attached specialists producing goods other than fish for a fishing lord.

Implications of the Botanical Data for Specialization

The botanical sample from the Late Horizon excavations at Lo Demás sheds light on some aspects of specialization at the site while leaving a number of ambiguities that must be resolved using other classes of data.

It would seem that some of the artisans mentioned in the "Aviso" (Rostworowski, 1970) were attached to local level lords, including fishing lords. The Sector IV cotton and gourd utensil manufacturers could well have been full- or part-time specialists working for the lord. If this was the case, it challenges the autonomous nature of all of the occupational specialists in Chincha suggested by the ethnohistoric model drawn exclusively from data on Chincha (*see* Chapter 2). However, given the generalized structure of authority and its exercise in the Andes (e.g., Netherly, 1977), it is not surprising that a model applied to the population at large should be warped within the orbit of lords exercising sufficient power to construct the monumental structures in Sector IV of Lo Demás. Indeed, such a case accords well with the general coastal ethnohistoric model drawn from the more detailed north coast record (*see* Chapter 2).

In Sector I, the residential area of common fishermen, the plant remains raise more questions than they answer. A large part of the identified remains pertain to wild species from the shoreline and from the marsh/backbeach habitat that used to lie between Lo Demás and the shoreline (*see* Chapter 5). Among these species, the most common are the various marsh reeds and canes, including the totora species necessary for making reed rafts. Traditional Andean fishermen today encourage stands of these plants in natural or man-made sunken gardens near the shore, and there is archaeological evidence that this pattern extends into the pre-Hispanic periods (e.g., Kautz and Keatinge, 1977; *see also* Chapter 12). Moseley (personal communication, 1985) has suggested that the fishermen controlled their essential means of production, including reeds for rafts and cotton for nets.

The key question in evaluating the nature of Chincha specialization, however, is not whether the fishermen controlled stands of wild or semi-domesticated littoral plants, but whether they actively cultivated fully domesticated plants. Unfortunately, it is precisely on this point that the botanical remains are ambiguous. From the documentary evidence, it is clear that each specialized group had access to products of the other groups. Thus, a variety of plants are expected in the fishing site. The plant parts found, however, should only include the utilized parts and those elements that are part of the "package" in which the plants are traded. Many of the plant organs found in Sector I of Lo Demás fit this criterion (e.g., maize kernels and cobs, beans and bean pods, lucuma pits). Where both edible seeds and attached elements are present, the number of the attached elements far exceeds the number of seeds to which they would have been attached (e.g., maize cobs vs. maize kernels). The one exception is cotton, which the fishermen may have grown in order to control their supply of this crucial product.

On the other hand, many of the recovered plant organs are optional parts of potential packages. The primary instance of this situation is the abundance of maize stems and leaves. If stems and leaves formed part of the unit by which maize was transported (Andean farmers usually do transport and store maize with the leaf and stem), then essentially all of the maize remains could have arrived at the site through exchange. Another possibility is that the maize leaves and stems were acquired intentionally as guinea pig fodder. If either of these possibilities obtains, then the plant remains do not contradict the hypothesis that the late pre-Hispanic inhabitants of Lo Demás Sector I were specialized fishermen. Future analyses of the Lo Demás guinea pig coprolites and comparison of the plant remains from contemporary, inland farming sites such as Huacarones will help resolve the remaining ambiguities.

CHAPTER 11

THE ARCHAEOLOGY OF LO DEMÁS

This chapter synthesizes the archaeological information on the Late Horizon fishing site of Lo Demás, in Chincha, Peru. These data come from the excavations in 1983 and 1984 (*see* Chapters 5 and 6) and from subsequent analyses of the recovered artifacts and organic materials (*see* Chapters 7 to 10).

Summary of Site, Layout, Excavations, and Stratigraphy

Lo Demás runs north–south parallel to the shoreline; at the time the site was occupied, most of the land around it was either marsh or a roughly contemporary cemetery. The site is divided into four sectors: Sector I (to the south) contains Late Horizon common residences, Sectors II and III have late pre-Hispanic burials and buried Paracas 9 (late Early Horizon) structures (*see* Figs. 3 and 4), and Sector IV contains parts of two late pre-Hispanic monumental structures, Buildings IV–1 and IV–2 (*see* Fig. 6).

Excavations were conducted in Sectors I, II, and IV, using natural strata; the Sector II results are not discussed in detail in this study. In Sector I, 22 m^2 were opened. Strata consisted mostly of primary midden deposits and use-trampled floors punctuated by pits and channels filled with refuse from overlying deposits. The strata and features fall into four major stratigraphic units (A to D, from bottom to top), of which B to D contain most of the remains, while A is nearly sterile. These complexes form the units of analysis for the artifacts and organic remains from Sector I. The organic remains (particularly fish and shellfish) show trends which help confirm the validity of the strata groupings, especially the difference between Complex C and Complex D.

In Sector IV, a partially destroyed room (IV–1a) in Building IV–1 was cleared and a 1 m^2 test pit was opened next to Building IV–2. This excavation continued to the base of the major construction episode of Building IV–2 but did not reach sterile soil. The test pit had 17 levels and several sublevels and features.

Limitations on the Data

The nature of the sample constrains the archaeological data from Lo Demás in several ways. First, the absolute size of the sample is small relative to the size of the site (and post-depositional destruction has significantly reduced the original extent of the site). Second, the sample is judgmental rather than random, so that I cannot determine statistically the degree to which the sample represents the site as a whole. Third, limitations on time and money made it necessary to sample the sample of organic remains from the Sector I excavations.

These limitations are mitigated in several ways. First, the entire eastern side of the site presents a continuous, quebrada-cut profile of the archaeological deposit. Visual assessment of this profile indicates that the excavated sample *is* generally representative of the site as a whole. The quebrada profile also allowed me 1) to place the Sector I excavation in the deepest part of the deposit, so that the sample covers the full temporal span of the site; and 2) to place the Sector IV test pit (Subunit 26D) in a location where it intersected refuse deposited directly from Building IV–2, so that the remains are indicative of activities carried out in that building. The quebrada profile also made it possible to determine the sequence and nature of the construction of Building IV–2 and, to a lesser degree, Building IV–1. Second, concerning the analyzed samples of organic remains from Sector I, visual inspection of the unanalyzed material from the rest of the excavation shows it to be quite similar to the excavated sample; furthermore, the analyzed sample from Sector I came from three different parts of the excavation yet showed consistent trends.

Chronology

Radiocarbon dates, pottery, figurines, pyroengraved gourd fragments, spindles and spindle whorls, and architecture provide information on the chronology of Lo Demás. The artifacts which can be assigned dates (discussed below) indicate that the entire occupation of Lo Demás took place during the Late Horizon, beginning at or about the Inka conquest of Chincha (ca. 1479 according to Menzel and Rowe, 1966), and ending shortly after the Spanish conquest in 1532. In other words, the occupation of the site probably spanned 50 to 60 years, from around A.D. 1480 to 1540–1550. Eight radiocarbon dates on charcoal from excavation contexts at Lo Demás support this estimate; discounting one anomalous result (*see* Chapter 5), the uncalibrated dates run from 475 ± 140: A.D. 1475 (BGS 1196) to 350 ± 80: A.D. 1600 (BGS 1191), with an average mean date of A.D. 1535 (*see* Fig. 60 and Table 3). Calibrated according to the curves published by Stuiver and Pearson (1986), the average mean date ranges from A.D. 1471 to A.D. 1486 (the variation results from radiocarbon readings that intersect the calibration curve more than once).

The chronologically diagnostic cultural remains include some which pertain exclusively to the Late Horizon and others which are related to Menzel's (1966) Chincha style, which she dated on the basis of gravelot seriation to the last epoch (8) of the Late Intermediate Period and the beginning of the Late Horizon (before the Inka conquest of Chincha). Late Horizon elements from Sector I include a Cuzco Polychrome A (Rowe, 1944) sherd (Fig. 29c) from the base of Stratigraphic Complex B (the lowest major complex), two plate fragments with a Late Horizon Ica 9 design from Complex B (Fig. 27a, b), an Inka-related painted spindle from Complex B, two sherds with a Late Horizon Ica Inka fish design from

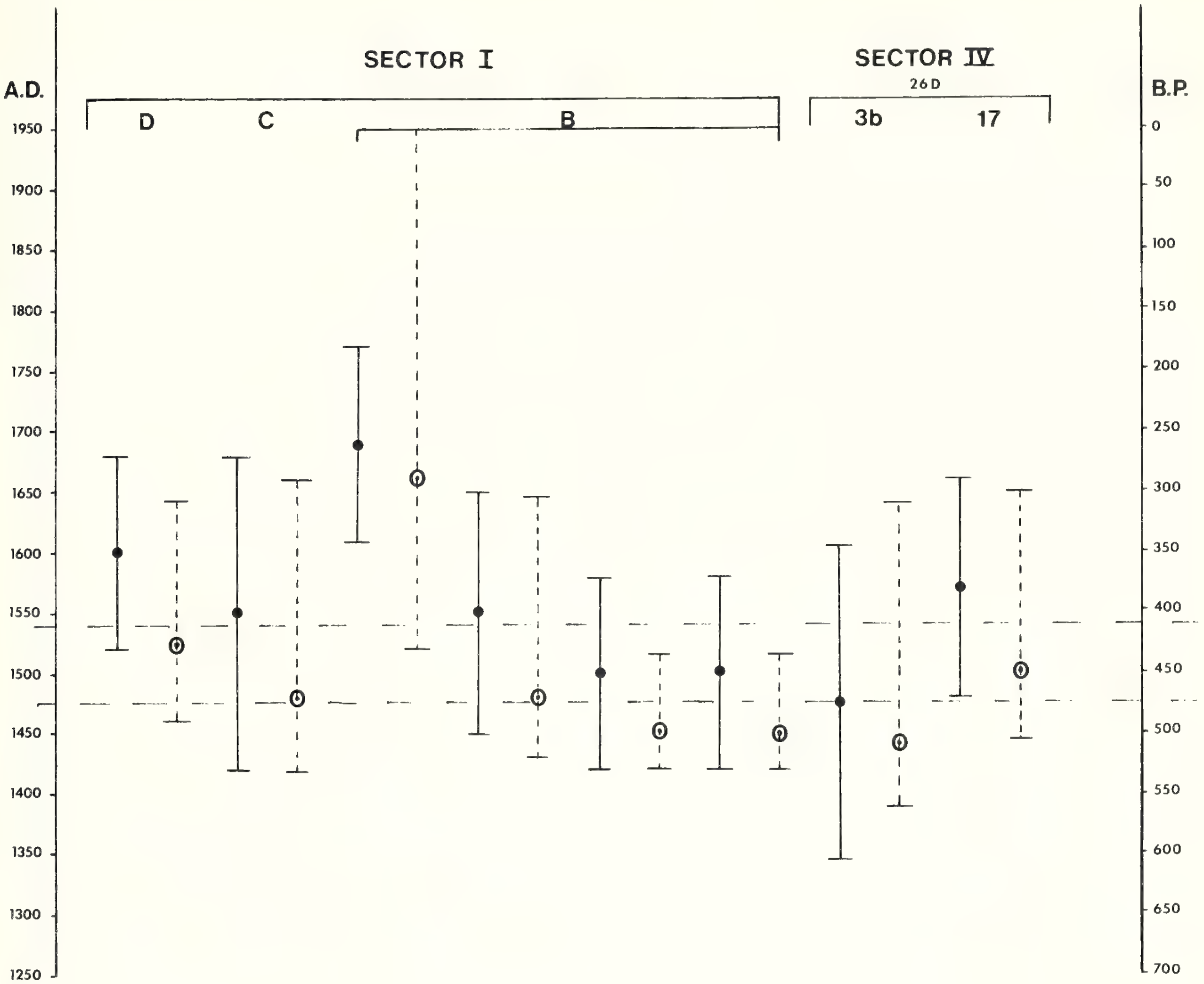

Fig. 60.—Radiocarbon dates from Lo Demás, run by the Brock University Geological Sciences Radiocarbon Lab (BGS) (*see* Table 3). Solid vertical lines are uncorrected dates, one standard deviation around the mean. Dashed vertical lines to right of solid lines are one standard deviation ranges for the same dates calibrated according to the tables published by Stuiver and Pearson (1986). The dashed horizontal lines bracket the best age estimate for Lo Demás based on the artifacts and the historical sources. Capital letters under Sector I refer to stratigraphic complexes; numbers under Sector IV are levels.

Complexes B and C (Figs. 29e, 30c), two pyroengraved gourd fragments from Complexes B and C with LH Ica 9 style decoration (Fig. 44a, b), two south coast Late Horizon style (Menzel, 1967) figurine fragments in Complex C (Fig. 34), several Pachacamac Inka blackware sherds from Complex D (Figs. 31o, p, 36), an Ica Inka sherd (Fig. 31g) from Complex D, a possible Cuzco Inka sherd from Complex D (Fig. 31h), and a *llanke* sandal from Complex D (Fig. 49). Two sherds from Complex D (the latest complex) have designs similar to Ica 10 decoration (Fig. 31e, f); Menzel (1967) places Ica 10 in the early Colonial Period, after the disruption of the Inka empire but before the advent of significant European influence. Together with a 1 × 1 cm piece of possible cowhide and one specimen of an Old World plant found near the top of Complex D, these sherds suggest that the occupation of Lo Demás ended early in the Colonial Period. The lack of European ceramics or other artifacts of any kind in the Lo Demás deposits indicates that the occupation of the site probably did not continue very long into the Colonial Period. Early post-conquest abandonment of the site makes sense given the extremely rapid depopulation at Chincha following the Spanish conquest (Cook, 1981:160).

Late Horizon elements in Sector IV include an Inka plate fragment from level 26–5 of Subunit 26D (Fig. 27c), a Provincial Inka sherd in level 26–13b in the same excavation (Fig. 32d), a Late Horizon spindle in level 26–5ci in 26D, and the rectangular *adobes* used in the construction of Building IV–2. These *adobes* are related stratigraphically to the lowest excavated level in Subunit 26D; together with the occurrence of Late Horizon artifacts in this excavation and in Sector I, this use of a Late Horizon, Inka-related architectural style demonstrates contemporaneity between Sectors I and IV. The radiocarbon dates (*see above*) support this conclusion.

Both sectors, however, also contain elements related to Menzel's (1966) LIP 8/early LH, pre-Inka conquest Chincha style. In Sector I, these elements include five rims with the Chincha Rim Scallop design feature distributed among Complexes B to D (Figs. 23p, r, s, 25a), a sherd with Chincha Ica decoration from Complex B (Fig. 29f), a Chincha style figurine from Complex C (Fig. 33), a sherd with a Chincha style textile fish design from Complex C (Fig. 30d), and several sherds from Complexes B and C with shoulder/neck banding, which may be a Chincha Ica feature (Figs. 29a, b, 30a, b). Another sherd with probable shoulder/neck banding came from Complex D (Fig. 31a). In Subunit 26D, Sector IV, Chincha style finds include several rims with the Chincha Rim Scallop design feature from levels 26–13b and 26–13bi (Figs. 23f, 25j), a sherd with shoulder/neck banding from level 26–16 (Fig. 32a), and a Chincha style figurine leg from level 26–14b (Fig. 38a). A Chincha style figurine (Fig. 37) was also found in the quebrada profile, in a level equivalent to level 26–12d.

A number of artifacts from the excavations at Lo Demás mix elements of both Chincha (Menzel, 1966) and Late Horizon styles. The spindle whorls fit Kroeber and Strong's (1924:32–33) shape criteria for Chincha style whorls, but paste and firing seem closer to their description of Late Horizon, Inka-related examples (Chapter 8).[113] One of the Late Horizon figurine fragments from Complex C in Sector I has some traces of Chincha style figurine features (Fig. 34a).

As the above lists show, the chronological markers from Lo Demás include elements related to Menzel's (1966) LIP 8/early LH Chincha style and to a variety of Late Horizon styles. The stratigraphic association of elements pertaining to these supposedly discrete units shows that the Chincha style was in use during the Late Horizon, as I have argued earlier in this study (Chapters 7 and 8). This discovery raises an important question: is the Chincha style as defined by Menzel (1966) *also* the pre-Inka, late Late Intermediate Period style of the Chincha valley, or is it temporally confined to the Late Horizon? I cannot answer this question definitively until more information is available from stratigraphic contexts which clearly pre-date the Inka conquest of Chincha,[114] but the data at hand provide some clues to the origin of the Chincha style. First, Uhle (1924; Kroeber and Strong, 1924; Menzel, 1966) found Late Horizon pottery along with Chincha style vessels and figurines in some of the burials which he excavated in Chincha. Menzel (1966) resolves this problem by extending the Chincha style into the early Late Horizon and proposing that Inka influence arrived before the Inka armies. This argument depends on demonstrating that all of the Chincha style burials without Late Horizon elements are earlier than those with LH material. Unfortunately, the information provided by Uhle (1924) was insufficient for Menzel (1966) to make this distinction.

Second, one of the most ubiquitous features of Chincha style pottery, the Chincha Rim Scallop (Menzel, 1966:92), is quite likely derived from an Inka design element—pendent triangles are a common feature of Inka ceramics. Six sherds from the Lo Demás excavations have the Chincha Rim Scallop design (Figs. 23f, p, r, s, 25a, j). Menzel (1976: 135) denies the Inka connection, as she must in order to maintain the chronological integrity of the Chincha style, noting a difference in the execution of Inka and Chincha pendent triangles (Menzel, 1976:146). However, if the Chincha Rim Scallop was borrowed from the Inka design, there is no reason to assume that the local imitation would be exactly the same as the source. For instance, Ica Inka ceramic decoration described by Menzel (1976) is not identical to the Inka source designs, nor are other styles recognized throughout the Andes as provincial Inka. However, Menzel also confirms that the Chincha Rim Scallop is a design feature which first appears in LIP 8 Chincha style ceramics (D. Menzel, personal communication, 1987). This fact argues in favor of the Chincha style as a predominantly Late Horizon pottery style with roots in the Late Intermediate Period (Sandweiss, 1992:41).

CULTURAL CONNECTIONS AND AFFILIATIONS

Many of the same data which provided clues to the chronology also help determine the cultural affiliations of the Late Horizon inhabitants of Lo Demás. Ceramics and figurines are particularly important in this respect. The Lo Demás assemblage includes items with Inka, Ica, and Pachacamac affinities, in addition to materials in the local, Chincha style.

In Sector I, Inka influence is seen in the presence of several potsherds in Inka or Inka-related styles, and of two figurine fragments found together in Complex C. Based on his analysis of Guaman Poma's drawings, Mejía Xesspe (1975–1976:37) believes that *llanke* sandals like the one found in Complex D were worn only by people of Inka affiliation. The pendent triangle design known as the Chincha Rim Scallop may also represent a local borrowing from an Inka design element (*see above*).

In Sector IV, both the presence of several Inka or Inka-related sherds and the use of rectangular *adobes* in Building IV–2 provide evidence of Inka contacts.

Contact with or influence from Pachacamac is seen in the blackware tuber-shaped vessel sherds and in the blackware faceneck sherd, all from Complex D in Sector I. Perhaps the most pervasive evidence of external contacts concerns Ica: a variety of potsherds from both sectors have designs related to Ica 9 and other Late Horizon Ica styles, as well as with presumably earlier Ica decoration; two pyro-engraved gourd fragments have Ica-like designs; and Building IV–1 in Sector IV is similar in architectural design and in decoration (geometric sea birds) to an Ica 10 house model pot from Ica (Fig. 18; *see also* Menzel, 1976:Plate 63–100).

The local, Chincha style (as defined by Menzel, 1966) occurs on potsherds and figurines from both sectors. I have argued above that this style persisted throughout the Late Horizon (and may have been significantly altered at the beginning of that period). However, Menzel's (1971) and Wallace's (1972) brief descriptions of pre-LIP 8 Chincha pottery suggest that the Chincha style *does* represent the local culture. More telling is the fact that Menzel (1966) was able to define a set of features unique to Chincha and to distinguish them from other late pre-Hispanic pottery styles. Regardless of the exact chronological placement of the Chincha style, its uniqueness supports Menzel's contention that it represents the local Chincha culture. I therefore suggest that the Late Horizon inhabitants of Lo Demás were natives of Chincha who maintained extensive contacts with other cultures/areas, and were not *mitimaes* colonists brought from elsewhere by the Inka.

SUBSISTENCE

Although I have not attempted to quantify the contribution of different plants and animals to the diet of the late pre-Hispanic inhabitants of Lo Demás, a qualitative assessment is possible.

The bulk of the meat consumed at the site clearly came from maritime species. Fish[115] and shellfish were most important in both sectors, but sea mammals and sea birds also provided some meat. The contribution of terrestrial fauna was limited; guinea pigs[116] were the principal terrestrial meat source in Sector I, while some camelids and cervids were consumed along with guinea pigs in Sector IV. Parallelling this conclusion from the bones, the animal coprolites show that while guinea pigs were kept in both sectors, live camelids were present only in Sector IV. The fish and shellfish also show a difference between the two sectors; the larger, Perciform fish and bigger individuals of the larger mollusks were more common in Sector IV than in Sector I. Furthermore, the Sector IV sample contains a higher percentage than the Sector I sample of shells from species which were not collected locally. These contrasts probably reflect differential or privileged access to resources on the part of the Sector IV elite residents.

Plant foods were also important in the diet at Lo Demás. Although some edible wild plants are present, field cultigens comprise the majority of the identified plant remains. The predominant plant organs recovered are either the edible part of the plant or else are elements which come attached to the edible portion. Among the edible plants, maize and peanuts predominate. In Sector I, peanuts are most common in the lower complex (B) and decrease in importance in the succeeding complexes (C to D). Maize shows the opposite trend, increasing in abundance through time and predominating in Complexes C and D. Coca is limited to Sector IV, providing further confirmation of the elite nature of that sector.

DOMESTIC ACTIVITIES

The excavations at Lo Demás found evidence for a variety of domestic activities. Most of the pottery was used for cooking, although it also seems to have been used for serving and eating, liquid containment, and storage (probably short term). The presence of several grinding stones suggests that some food was processed by grinding. Food processing may also have been done using expediently produced and highly expendable cobble cortex flakes. Other household activities which probably took place on a daily or frequent basis include raising guinea pigs, spinning, sewing (to patch and perhaps make clothes), and possibly weaving. Wood fragments, often with cut marks, show that woodworking was carried out at the site, perhaps to make the wooden tools which we found in the excavations. Pieces of polychaete worm calcareous heads were probably used as woodworking rasps. Both sectors (I and IV) contain indicators of all of the activities listed in this paragraph.

Fishing and Fish Production

Several lines of evidence indicate that fishing and fish processing were important activities in Sector I of Lo Demás, though not in Sector IV. Five net fragments were visible in stratigraphic position in the quebrada profile immediately to the east of the Sector I excavations, and we found 85 fragments distributed throughout Complexes B to D, the main occupation levels of the excavation. The small average mesh size is appropriate for *anchoveta* and sardine, which are the two predominant fish species in the deposits. The fact that nets and net fish predominate also argues for large-scale "industrial" fishing to produce fish in quantity for tribute and/or exchange as well as for local consumption.

Among the scarce manufactured artifacts found in the excavations was a *mallero,* or net-gauge, a wooden implement used to make and repair nets. Fishermen in Chincha today repair their nets with wooden *malleros* like the Lo Demás specimen; this activity takes place in front of the fishermen's houses, and the broken fragments are discarded in the street in a manner analogous to the archaeological net fragment occurrences at Lo Demás. According to local fishermen, the *mallero* recovered from Lo Demás would produce nets with a mesh size similar to the excavated fragments. Bone needles found in Sectors I and IV may have been used for netting, as they are too large for ordinary textiles.

In Sector I, we also found a small copper hook and 12 of the half-bobbin objects. This latter category of artifact may be related to fishing, given its known distribution. Cobble cortex flakes from Sector I show use wear which may have resulted from scaling and cleaning fish; one still had fish scales adhered to it. Such flakes are fairly abundant in this sector, although only a few were analyzed (Kvietok, 1988).

The most common skeletal elements of fish in the study sample from Sector I were various disarticulated cranial bones; we also found 84 intact fish heads. Gills appeared in abundance in several levels. Gills and internal organs are the first parts of a fish removed after capture to increase preservation, while heads would be removed from salted and/or dried fish intended for exchange in order to reduce weight and bulk. Tests for salt content in the periosteum of fish bone from Sector I of Lo Demás revealed more salt on the fish than on other animal bones from the same contexts (Altamirano, 1984), suggesting preservation of fish by salting and drying. This suggestion must be tested through further lab work.

In the 1983 test pits in Sector I, excavation revealed a series of post holes and channels dug into Complex A from Complex C. These holes formed a pattern analogous to a modern fish salting and drying workshop in Tambo de Mora, again suggesting that salt fish production was carried out at Lo Demás. Two mats associated with fish scales and salt may represent another method of fish salting and drying, similar to a technique documented earlier in this century. These mats came from Complex C.

In Sector IV, disarticulated cranial elements and intact crania were common but not as frequent as in Sector I (41.5% by NISP in Sector IV, as opposed to 60.8% in Sector I). The Sector IV test pit (26D) had no net fragments or indications of fish salting or drying, although we did find a bone tool which resembles a *mallero,* a possible bone netting needle, and seven half-bobbin objects, including the only articulated specimens from Lo Demás. Based on the limited sample from Sector IV, if the residents of this elite sector fished, they do not seem to have done so with the same intensity as the residents of Sector I.

Production Other Than Fish

The excavations in Sector I provided abundant evidence for the consumption or use of products other than fish—plant foods, pottery, textiles, and metal—which do not seem to have been produced by the inhabitants of this sector. Indeed, the utilized resource and tool inventories provide evidence for only one kind of production other than fishing and the domestic activities discussed above; the abundance and types of cotton remains suggest that the Sector I residents may have grown cotton for their nets, for thread, and possibly for weaving cloth. The botanical remains also indicate that the inhabitants of Sector I harvested (and perhaps encouraged) stands of wild marsh plants, especially reeds. Reeds could have been used for boats, as well as for the walls and matting documented in the Sector I excavations and quebrada profile.

The situation in Sector IV is quite different. Evidence for fishing and fish production in the Subunit 26D sample is less than in the Sector I samples, but the Sector IV botanical remains provide very strong evidence for the production of gourd utensils in Building IV–2. It may be that gourd utensil production was a by-product of gourd acquisition or even cultivation by the fishermen, who would have used whole gourds as net floats (J. Quilter, personal communication, 1991). The Sector IV botanical remains offer stronger evidence than in the Sector I sample for cotton fiber processing and for woodworking, although the artifact inventory indicates fiber processing in both sectors.

The Pachas collection of metal pieces from Sector IV and the surface collection from the bluff to the north of Lo Demás suggest that a metallurgical workshop was located somewhere in the vicinity of the site, though the lack of slag deposits in the surviving portion of Lo Demás argues against the workshop being located in the immediate vicinity of the site as it now exists.

Curanderos and Ritual Activities

The Sector I remains indicate another kind of activity carried out by a full- or part-time specialist: curing. The guinea pigs in Complexes A to C provide the strongest evidence for a *curandero* at the site; these animals had had their stomachs slit but had not subsequently been eaten. Use of guinea pigs as diagnostic devices in curing rituals both today and in late pre-Hispanic times involves rubbing the patient's body with a live guinea pig and then cutting the animal's stomach open to inspect the entrails (e.g., Arriaga, 1968 [1621]:210; Bolton and Calvin, 1981:315–316). This ritual produces guinea pig corpses identical to those found at Lo Demás.

The botanical remains provide further evidence for the presence of a *curandero* in Sector I; the sample from that sector has over 50% more medicinal plant species than the sample from Sector IV, even though the samples are comparable in size (NISP). The presence of masticated dicot fibers in the stomach contents of a late pre-Hispanic burial in Sector II also argues for a curer in the area.

The broken figurines and the interment of bird corpses beneath floors and walls provide further evidence of ritual activity in Sector I, though these finds do not indicate whether that activity involved ritual specialists.

Intraregional and Long-Distance Exchange

The list of products found in Lo Demás which do not seem to have been produced by its inhabitants (*see above*) indicates the kinds of items which were circulating through local exchange (or redistribution) in Late Horizon Chincha. The Lo Demás samples also provide limited evidence of intraregional (sensu Netherly, 1977:Chapter VI) and long-distance exchange and some information on the modes of transport used by the long-distance traders.

Some of the less common mollusk species found in Lo Demás did not come from the shoreline in the vicinity of the Chincha valley, but rather must have come from some distance to the north or south (Paracas, the Chincha Islands, or the coast between Chincha and Cañete). The rare sea mammal bones would also have come from animals killed in these areas. The presence of these species is evidence of intraregional exchange. However, "exchange" may not be the proper term here, as the Chincha fishermen could have travelled to the areas listed above to hunt or collect (rather than exchange for) the sea mammals and shellfish; early in this century, Tambo de Mora fishermen still regularly visited the Chincha Islands (Murphy, 1921).

The foreign pottery in Lo Demás must have arrived there as the result of long-distance exchange (however administered) with Ica, Pachacamac, and possibly Cuzco. My impression is that the Cuzco Polychrome A sherd from Sector I (Fig. 29c) is a local imitation, given the coarse temper, weak paint colors, and somewhat irregular design execution. On the other hand, the bright colors and sharply delineated, carefully executed design on the Inka plate fragment from Sector IV (Fig. 27c) suggest that this sherd is from an imported vessel. The exact concordance in form and decoration between the blackware faceneck jar from Sector I and vessels from Late Horizon Pachacamac argues in favor of the Lo Demás piece being an import. The blackware tuber pot sherds (Fig. 31o, p) from Sector I also appear to be imports; other tuber pots known from Chincha are oxidized, while a Pachacamac example is reduced-fired. Furthermore, the two Lo Demás tuber pot sherds are thinner and more delicate than almost all of the other pottery from the site, indicating a separate source, or at least a different production process. The Pachas metal collection from Sector IV of Lo Demás may represent trade goods, although the copper was probably worked and possibly mined locally.

The three bits of the warm water mollusk *Spondylus* were certainly acquired through long-distance exchange, as this species is almost never found south of the Peru–Ecuador border. One of the more intriguing questions about Chincha archaeology is why this species is not more abundant in late pre-Hispanic sites, considering that the ethnohistoric evidence is usually read as indicating that *Spondylus* (*mullu*) was the most important item acquired in the north by the Chincha merchants (Rostworowski, 1970). The excavations at Lo Demás confirm the scarcity of *Spondylus* in Chincha and provide indirect evidence to support the hypothesis advanced in Chapter 2 that the Chincha merchants acted as agents of the Inka and not as independent entrepreneurs.

Two pieces of evidence from the excavations at Lo Demás are pertinent to the transportation aspect of long-distance trading. First, the abundance of camelid excrement in Sector IV demonstrates that live camelids were brought into this part of the site. At the same time, the relative scarcity of camelid bones in the midden and the infrequent use of wool in the Lo Demás textiles indicate that these animals were not often butchered or sheared at the site. The best explanation for their presence is that they were used to transport something into and/or out of the site (*see* Chapter 12 for a further consideration of this matter).

The second piece of information about long-distance transport concerns the construction of a jetty on the shoreline in the vicinity of Lo Demás at the beginning of Stratigraphic Complex D (Sector I). The presence of a jetty would explain the reversal in dominance of the sand-dwelling clam *Donax* and the rock-dwelling mussel *Semimytilus* between Complexes C and D, and would accord (to a lesser degree) with a similar trend in the two dominant fish species, *anchovetas* and sardines. Loading and unloading large trading rafts on the open Chincha shoreline would have required a jetty or similar construction. Such a facility built to service the lord of Chincha's ethnohistorically documented long-distance trading activities would be located close to Lo Demás, because the site lies almost directly between the sea and La Centinela (*see* Fig. 1). It is probably not coincidental that the series of cobble and mud mortar walls which cover Sector I of Lo Demás—the most complex architecture in that sector—were built at the start of Complex D. Also, the Pachacamac–Inka potsherds imported from the central coast of Peru occurred only in Complex D.

ELITE AND COMMON RESIDENTS

One theme which has run through much of this chapter is the evidence that Sector IV was occupied by people who held an elite status relative to the inhabitants of Sector I. The most direct indication of this status hierarchy is the architecture; Sector I contains small, ephemeral structures, while Sector IV consists of large, monumental structures, at least one of which has painted decoration (Room IV–1a in Building IV–1). As Moseley (1975) and others have argued, the construction of monumental buildings requires some people with sufficiently high status to mobilize the necessary corporate labor groups.

The two sectors differ in other ways, as well. In terms of diet, Sector IV had more large fish, shellfish, terrestrial mammals, and coca than did Sector I, indicating privileged access to these resources by the Sector IV residents. In Sector I, economic activities were confined to fishing, net manufacture and repair, fish processing, and domestic chores—the daily routine of fishing families throughout the world. In contrast, the Sector IV residents seem to have concentrated less on fishing but to have carried out artesanal production of gourds, cotton products, and perhaps wooden objects.

Finally, the presence of Inka type rectangular *adobes* in Sector IV walls indicates a closer connection with the Inka administrators of the valley. Few sites in the valley aside from the Inka administrative center at La Centinela have structures made of these *adobes*. The best candidate for an imported Cuzco Inka sherd[117] also came from Sector IV.

Given all of the data pointing towards the elite nature of Sector IV, I conclude that it was probably the residence and center for a fishing local level lord.[118] The identification of status differences between the two sectors at Lo Demás provides the key to determining between the ethnohistoric models presented in Chapter 2 and evaluated in the following, concluding chapter.

CHAPTER 12

LO DEMÁS AND THE ARCHAEOLOGY OF SPECIALIZATION ON THE ANDEAN COAST

The ethnohistoric record for the Andean coast at the time of the Spanish conquest indicates quite clearly that occupational specialization was an important mode of socioeconomic organization. For the Chincha valley, however, the documents do not provide a wealth of details concerning the organization of specialization, nor do they speak about daily life and local interactions. The record for the north coast of Peru offers more information on the organization of specialization (though the details of daily life remain obscure), but we cannot assume a priori that the north coast and the south coast (Chincha) were necessarily alike. The differences in the ethnohistoric models of specialization among late pre-Hispanic coastal fishermen could reflect real differences in organization, and not simply the smaller number of sources available for Chincha. Furthermore, the ethnohistoric record in general cannot be taken as an unbiased one; the native informants may have had reasons to misrepresent their economic and associated sociopolitical structure, and the Spanish observers certainly brought their own personal and cultural backgrounds and biases to their interpretations of what they observed and were told. In this context, a source of information independent from the ethnohistoric record is necessary to evaluate and contrast the different document-derived models.

Although archaeological data and interpretations have biases and problems of their own, they are not subject to informant misrepresentation, and therefore can provide independent tests of the models derived from the documents. It was with these concerns in mind that I designed and executed the Chincha Fishermen Project as an archaeological study of later pre-Hispanic coastal specialization. The target population consisted of a group of fishermen for whom the ethnohistoric record offers several pieces of information crucial for such a study: the population was occupationally specialized, residentially discrete, temporally constrained (late pre-Hispanic through early Colonial Period), geographically located, and physically described.

This concluding chapter evaluates the correspondence between the ethnohistoric and archaeological records for the fishermen of Chincha, assesses the archaeological data concerning specialization in terms of the ethnohistoric models described in Chapter 2 and according to the criteria discussed in Chapter 3, and places the results of this study in the context of other archaeological studies of later pre-Hispanic coastal specialization.

LO DEMÁS AS THE CHINCHA FISHERMEN'S SETTLEMENT

Identification of Lo Demás as part of the Chincha fishing settlement was necessary before the archaeological data from the site could be used to assess specialization. The orientation of Lo Demás parallel to the shoreline and extending north from the vicinity of La Centinela fits the documentary description for the location of the fishing settlement, and the long, narrow configuration of the site corresponds to the "Aviso" statement that the settlement "looked like a road." The chronology of Lo Demás—Late Horizon to early Colonial Period—is appropriate. The abundant evidence that the inhabitants of the site fished, processed fish, and hunted or collected other maritime resources confirms that they were fishermen, whatever other specialized or nonspecialized activities they may have carried out. There is little doubt that Lo Demás was, indeed, part of the fishing settlement described in the "Aviso" document (Rostworowski, 1970).

SPECIALIZATION AT LO DEMÁS

In Chapter 2, I reviewed the ethnohistoric data for late pre-Hispanic Chincha and for the north coast of Peru. I used these data to derive to models of economic organization for the fishermen, Model One based exclusively on the Chincha sources and Model Two incorporating the north coast record. In Chapter 3, these models were discussed in terms of four parameters of specialization (context of production, concentration of productive activities, constitution of production units, and degree of specialization [Brumfiel and Earle, 1986; Costin, 1986]) and a set of archaeological expectations was formulated for each of the two ethnohistoric models.

According to Model One, the Chincha fishing settlement should have evidence for fishing but not for any other class of production. This fishing evidence should be evenly dispersed throughout the site. The settlement should contain both commoner and elite sectors and should have some evidence of links with the Inka state and the paramount lord of Chincha. Expectations for Model Two differ in that the elite sectors should have evidence of auxiliary specialists attached to the fishing lords; in the commoner sectors, evidence for fishing should still be evenly dispersed. Links to the governing elite/institutions are still expected. According to both models, the fishing settlement should contain products obtained through exchange with other local producers. Both models also suggest that the fishing settlement should show temporal continuity of group identity.

The most important archaeological information for evaluating and contrasting the ethnohistoric models is the differences between Sectors I and IV, interpreted respectively as the loci of common fishermen and of fishing lords and their retainers. The commoner inhabitants of Sector I seem to have concentrated on a single productive activity—fishing—while the elite residents of Sector IV had attached specialists, in accordance with Model Two.

Excavations in Sector I found indications that many of the nonmarine products in the site were acquired from other producers, but no evidence of nonfishing production. Fishing tools include net fragments, a hook, and a net-making tool. Fish remains include branchia and abundant cranial elements (including whole heads), which suggest that fish were processed for trade as well as consumed at the site. Evidence for several methods of fish salting supports this assertion.

The plant remains from Sector I consist mostly of edible parts and elements which come with edible parts in a natural package (e.g., corn kernels and cobs), and the tool inventory does not include farming tools. These facts argue that the site's inhabitants did not farm. The location of the site away from areas which could have been agricultural fields during the late pre-Hispanic occupation of Lo Demás also argues against the occupants having been farmers, as do the differences between the pottery assemblage from Lo Demás and that from Huacarones, a contemporary farming site. However, the Sector I inhabitants may have grown some cotton for their nets and thread, and they also seem to have harvested wild marsh plants, mainly reeds for use in construction, matting, and possibly boats. Furthermore, the inhabitants of Sector I carried out a variety of domestic activities including cooking, spinning and sewing, woodworking, and raising guinea pigs. One (or more) of the Sector I residents seems to have been a *curandero,* which would have required at least part-time specialization. The excavations in Sector I found several potsherds and figurine fragments which indicate direct and/or indirect links with the Inka and with other Late Horizon coastal centers such as Pachacamac. Pachacamac was probably the most powerful coastal shrine during and before the Inka occupation of the central Andean coast. The ethnohistoric data indicate that Chincha had a special relationship with Pachacamac, so it is not surprising to find archaeological evidence of contact. The Uhle collection from Chincha also contained Late Horizon pieces from Pachacamac (Menzel, 1966).

In contrast to the commoner nature of Sector I (as indicated by the architecture and the organic remains), Sector IV was occupied by elites, probably a local level fishing lord and his retainers.[119] The archaeological sample from this sector does not provide much evidence for fishing and fish processing, but it does indicate that other categories of nondomestic production took place in the elite sector.

The abundance of cotton remains in Sector IV suggests a greater emphasis on fiber processing than in Sector I. This find is interesting in light of the discovery of a textile-processing area in the Inka sector at the nearby site of La Centinela (Morris, 1985; *see* Fig. 1). The Lo Demás Sector IV sample came from Building IV–2, which was built of rectangular *adobes*—an Inka architectural feature. These data suggest that fiber processing in Chincha, at least on a large scale, was carried out under the supervision of the elites, particularly those associated with the Inka; this conclusion is not surprising considering the importance of cloth in the Inka world (Murra, 1962, 1980).

The botanical remains provide clear evidence of another kind of production in Sector IV: the manufacture of gourd utensils. It is unclear whether these gourds were intended for use by the local lord (perhaps as a substitute for scarce pottery), for exchange, or both. Several early sources mention gourds as one of the important items traded by Chincha merchants (Rostworowski, 1970:156–157).

The Pachas metal collection from Sector IV of Lo Demás and the surface finds from the bluff north of Lo Demás indicate that there was a metallurgical workshop producing copper objects somewhere on the north side of the valley. This workshop may also have been located in the domain of the fishermen and, like the gourd and textile workers of Sector IV, attached to the fishing lord.

The abundant camelid dung in Sector IV (and its absence from Sector I) suggests that the fishing lord shipped some products by llama. The scarcity of wool textiles and the small number of camelid bones in the subsistence remains leave transport as the most likely function for the camelids which deposited the dung. Most likely, the cargos included items for exchange, as well as the tribute paid to the Inka and perhaps to the paramount lord of Chincha. If the documents are correct and each specialist paid tribute in the "things of his office," then fish should have composed the bulk of the cargos. Gourds and perhaps metal objects might also have been sent. The archaeological sample from Sector IV sheds no light on this problem, but analogy to work by Marcus (1987*a*, 1987*b*) at the nearby fishing site of Cerro Azul suggests that fish *were* the major cargo—Marcus found camelid dung scattered throughout a room near the entrance to a rectangular compound; this compound had storerooms full of dried fish.

Although the excavated pottery from Sector IV is too scarce to offer more than (strong) hints, the architecture of this sector shows clear links with the Inka. Indeed, Lo Demás is one of the few Chincha sites with Inka-related architectural features, other than the Inka administrative center at La Centinela. This fact may show a particular desire on the part of the Inka administrators to forge links with the fishing lords.

There is no apparent hiatus during the occupation of Lo Demás, and the site contains pottery and other artifacts in the local style. The earliest construction phase in Building IV–2 (below the base of test pit 26D) may be Late Intermediate Period in date. These facts argue in favor of temporal continuity in fishing group identity, one of the expectations for both ethnohistoric models. On the other hand, the absence of pre-Late Horizon deposits in Sector I and the major reconstruction of Building IV–2 early in the Late Horizon suggest a significant change in the distribution of the Chincha fishing population at the beginning of the Inka occupation. In Sector I, increasing maize abundance in the upper stratigraphic complexes (C and D) and the construction of more formal architecture (cobble and mud mortar walls) at the start of Complex D may reflect an improvement in the economic status of the fishermen during the course of the Late Horizon.

In summary, the archaeological data from Lo Demás suggest that the common fishermen were specialized, but that their life did not consist simply of fishing, dancing, drinking, and "lo demás." In addition to the demands of daily life (of the sort not mentioned in the documents), these fishermen also made many of their tools and possibly cultivated or encouraged stands of the plant resources needed for these tools. In contrast, the fishing lord probably did not fish at all, but instead supervised specialized craft production of gourd utensils, fiber products, and possibly metal. The lord was also responsible for sending his subjects' tribute (fish? gourds? metal objects?) by camelid to the Inka administrators of the valley, with whom he seems to have maintained close relations. The lord probably also organized local and/or long-distance exchange.

The work at Lo Demás suggests that ethnohistoric Model Two applies to the Chincha fishermen. The strict specialization suggested by the Chincha documents (Model One) applies best to non-elite members of the specialized groups, in contrast to the associated elites. Even the non-elite specialist groups could include full- or part-time individual specialists such as *curanderos.* Within the orbit of the elites, the strict specialization model (One) breaks down, at least partly; specialist lords could have attached craft specialists producing commodities not related to the specialty of the lords' other subjects.

The null hypothesis for the Chincha fishermen (no specialization) denies validity to any of the ethnohistoric sources, all of which argue for some kind of specialization. Because the archaeological data fit the expectations for one of the ethnohistoric models quite well, I reject the null hypothesis.

SPECIALIZATION ON THE ANDEAN COAST

The ethnohistoric data on coastal specialization raise an important question which cannot be answered directly with the evidence from Lo Demás—was specialization an old tradition on the coast when the Inka conquered it, as Rostworowski (1970, 1977, 1981) believes, or was it an Inka invention or modification of some other pre-existing system? The Chincha documents do not discuss the nature of pre-Inka economic organization. The ethnohistoric record for the north coast suggests that the system of specialization seen in Model Two *is* pre-Incaic; the areal extent of fishing specialists on the north coast, and the fact that the fishing lords who are named have names in coastal languages, argue for the antiquity of fishing specialization (*see* Hart, 1983; Netherly, 1977; Ramirez-Horton, 1982; Rostworowski, 1981). However, only archaeology has the potential to answer definitively the question of origins. Therefore, the following paragraphs briefly review the archaeological data for fishing specialization from other coastal sites in the central Andes. This review concentrates on Late Intermediate Period and Late Horizon sites in order to address the role of the Inka in coastal specialization. I focus on fishing specialization because 1) it is the category of full-time specialists (those who did not plant fields) that is best documented in the ethnohistoric record, and 2) data from fishing sites are most comparable to the results from Lo Demás.

Because the earliest documented occupation in Sectors I and IV at Lo Demás dates to the Late Horizon, after the Inka conquest of Chincha, this site does not aid in assessing the *origin* of coastal specialization. A related problem is the possibility that Lo Demás represents a group of *mitimaes* moved to Chincha by the Inka as part of an empire-level archipelago. However, the fact that pottery, figurines, textiles, and other artifacts are more frequently decorated in the local, Chincha style than in any foreign style argues that fishermen were local, Chincha folk, even though the fishing settlement at Lo Demás dates entirely to the Late Horizon.

Cerro Azul, in the Cañete valley, is the excavated late pre-Hispanic fishing site closest to Lo Demás, and the one which provides the best evidence for pre-Inka fishing specialization. Although originally excavated in the 1920s by Kroeber (1937), only the recent work by Marcus (1987*a*, 1987*b*) offers information useful for assessing fishing specialization. Marcus's excavations concentrated on a Late Horizon Inka structure (not related to fishing) and on two large Late Intermediate Period structures (Structure D and Structure 9) (*see* Chapter 7 for a possible problem in dating the Cerro Azul site). Both of the latter two buildings had rooms which had been devoted to fish storage (mostly *anchovetas* and sardines), and in Structure 9, the number of rooms used for this purpose increased through time. Marcus considers Structure 9 as the center of a low-level administrator and Structure D as an elite residential compound, but one which also housed a number of other activities. She found evidence of two major activities in Structure D in addition to fish storage—weaving and plant drying and processing. Two rooms in this structure were devoted to raising guinea pigs, and a patio at the entrance to the compound contained abundant llama feces.

Comparison of the activities carried out in Structure D with those documented for Building IV–2 at Lo Demás (also a large, rectangular, elite residence and/or workspace) reveals a number of similarities. The llama dung at Lo Demás indicates that some cargo was carried out of Sector IV; given the evidence from Cerro Azul, that cargo may well have included fish stored inside Building IV–2. Fishing artifacts from Cerro Azul included net fragments, net weights, and a wooden *mallero.* This tool inventory is similar to that from Lo Demás. The list of plants and plant parts reported by Marcus (1987*b*:61) from a midden deposit in Structure D is similar to the botanical materials from Lo Demás, although more exact comparison must await the publication of the complete list from Cerro Azul. Maize and cotton were the most important species there, as at Lo Demás. Marcus (1987*b*:61) writes that the

> "presence of such varied plant parts suggests that Cerro Azul's corn and cotton probably did not come from very far away; but it does not necessarily rule out the possibility that those products were obtained from neighboring farmers, rather than having been grown by the occupants of Cerro Azul."

Though limited by its focus on the elite sector of the site, the Cerro Azul work supports ethnohistoric Model Two for the economic organization of the fishermen, rather than the strict specialization of Model One.

If Marcus (1987*a*, 1987*b*) has correctly dated Structures D and 9 at Cerro Azul to the Late Intermediate Period, before the Inka conquest of Cañete, then this site offers strong support for Rostworowski's hypothesis that specialization is a pre-Inka tradition.

No Late Intermediate Period or Late Horizon sites pertinent to the question of fishing specialization have been excavated on the central coast of Peru. On the north coast, a number of sites offer relevant information; however, none provides as clear a picture as Lo Demás or Cerro Azul, despite the fact that the most detailed ethnohistoric evidence for fishing specialization comes from the north coast.

In the Moche valley, Keatinge (1975) excavated a Late Intermediate Period assemblage at Cerro La Virgen in which the subsistence remains included seafood and agricultural produce, as at Lo Demás. Information on the species and plant or animal parts represented in the deposits is not provided. The artifactual evidence at Cerro La Virgen clearly indicates fishing (nets, hooks, and sinkers) and the "total spectrum of weaving activities from resource procurement to finished product" (Keatinge, 1975: 224). These data concord well with the evidence from Cerro Azul and Lo Demás.

Keatinge also uses two lines of evidence to propose that the site's inhabitants farmed as well as fished. First, he cites the proximity of the site to a large complex of state-built fields (Keatinge, 1975: 224). This criterion is not conclusive, as ethnohistoric data such as the "Aviso" for Chincha (Rostworowski, 1970) suggest that fishing settlements could be located in the fertile valley bottoms where agriculture was also carried out. Second, Keatinge (1975: 225) found "numerous donut-shaped stones which probably served as mace-heads or, more likely, as weights for digging sticks used in farming." One of the illustrated examples of these artifacts (Keatinge, 1975:Fig. 16–I) is identified in the figure caption as a possible net weight; this specimen has a smaller perforation than the rest. The differentiation between net weight, mace-head, and digging stick weight is crucial, as only the latter category would provide conclusive evidence that the inhabitants of Cerro La Virgen engaged in farming as well as fishing; Keatinge does not present any further evidence to indicate farming at the site.

Another problematic, late, north coast site is Medaños La Joyada, located in the desert between the Moche and Chicama valleys and adjacent to a number of sunken gardens. Moseley and Mackey (1972: 77) had identified this site[120] as a "totora fishing" settlement whose inhabitants grew totora reeds for their boats in the sunken gardens, fished, and acquired other agricultural products through exchange with inland farming sites. Kautz and Keatinge (1977) excavated at Medaños and report a set of artifacts similar to Cerro La Virgen: spinning and weaving tools, nets, net weights and floats, fishhooks, and "a partially drilled digging stick weight" (Kautz and Keatinge, 1977:89). European artifacts were also encountered, which "strongly suggests that at least some parts, if not the entire site, were occupied during the Colonial Period." In addition to excavation in the habitation area, trenches were dug in midden deposits around the sunken gardens. The remains included seafood, terrestrial animal bones, and agricultural produce. Pollen analysis revealed a high proportion of maize pollen, which Kautz and Keatinge (1977:92) believe indicates "that corn was grown, stored, and consumed at the site with little, if any, importation." Totora pollen was fairly low in frequency. The investigators therefore conclude that the inhabitants of Medaños la Joyada "participated in a broadly based subsistence economy which very likely included the cultivation of numerous crops in addition to totora (*Scirpus* sp.) as well as the exploitation of marine and littoral resources" (Kautz and Keatinge, 1977:95). These conclusions are tenable if, as Kautz and Keatinge suggest (1977: 90), maize was *not* "imported to the site with both husk and tassel intact." Maize tassels would have provided the large amount of maize pollen found in the site.

Donnan and Moseley (1968) report on the Late Intermediate Period site of Loma Lasca in the Santa valley, 400 m from the shore. Basalt cobble flakes and fish bones and scales were the most abundant remains at the site, while edible plant debris, animal and bird bone, shells, cordage, pottery, and net fragments were also present. The excavators characterize Loma Lasca as a fishing community, and state that "contemporary sites in the Santa valley tend to be located inland away from the coast" (Donnan and Moseley, 1968:503). Though lacking in detail, Donnan and Moseley's data and observations resemble the data from Lo Demás, particularly from the Sector I common residences.

Elsewhere, I have discussed the evidence for fishing specialization during periods preceding the Late Intermediate Period (Sandweiss, 1986), and will not review it here. It is worth noting, though, that the best evidence for early fishing specialization dates to the Initial Period and early Early Horizon on the north coast (Pozorski and Pozorski, 1979*b*, 1987). The lack of evidence for specialization in the intervening span (Early Horizon through Middle Horizon) probably reflects the lack of work in fishing settlements dating to these periods.

To synthesize this rapid review of the archaeological evidence, it appears that specialized fishing settlements pre-date the Inka conquest of the Peruvian coast and that the economic organization of these settlements concords with ethnohistoric Model Two. Fishing specialization does seem to be an old tradition in the Andes, dating at least from the Initial Period, but it is not yet clear whether the early, pre-Late Intermediate Period settlements included craft specialists attached to fishing lords. Presumably, attached specialists could only exist after the appearance of a political hierarchy involving local level lords. When this development took place is still a matter of some debate.

CONCLUSION

In view of the results presented here and in Chapter 11, it is worth considering briefly some of the implications of fishing specialization and its role in the incorporation of the coast into the Inka empire. In doing so, we must keep in mind that most of the conclusions are drawn from a small sample in one segment of the original Chincha fishing settlement. We need a still larger sample from that settlement, as well as samples from other sectors of the Chincha polity (such as those being excavated by the Chincha–Pisco Project) in order to test the reconstruction of later pre-Hispanic Chincha socioeconomic organization presented in this monograph.

The ethnohistoric and archaeological data for the north coast of Peru suggest that the Inka did not create the fishing *parcialidades* (social units) ab ovo. Rather, it seems that the fishing specialists were traditional coastal groups which the Inka subsumed into their empire without major changes in socioeconomic organization. As highlanders, the Inka would not have been likely to engage directly in ocean fishing or in long-distance raft trading and would probably have left the organization of such activities to those with the traditional knowledge necessary to manage them. For instance, Inka fishermen *mitimaes* were drawn from coastal polities, not from highland groups (Rostworowski, 1978:127–129). At Lo Demás, many of the artifacts which indicate cultural affiliation are in the local Chincha style, suggesting that the office of fisherman in the Chincha valley was carried out by the local inhabitants, and that the socioeconomic organization of the fishermen pre-dates the Inka conquest of the valley—even though the excavated portion of the site postdates the arrival of the Inka and does not provide direct evidence for pre-Inka organization. Perhaps the valley floor once held traces of earlier fishermen; the "Aviso" states that the Late Horizon fishing settlement extended across the entire valley. For the moment, we must look to the neighboring Cañete valley, where Marcus (1987*a*, 1987*b*) has found evidence of large scale fish production and probably specialization in the Late Intermediate Period component of the Cerro Azul site.

Nevertheless, the Inka did modify the coastal system to facilitate their control. As argued in Chapter 2, the Inka probably took the long-distance raft trading franchise away from the north coast Chimú and gave it to Chincha. The Lo Demás data suggest that the Inka actively forged links with the fishing lords; presumably, such links were part of a strategy to create direct relations of dependence with the various segments of the Chincha polity, bypassing the local paramount lord.

Based on the data, reviews, and analyses presented in this study, I argue that when the Inka incorporated the coast into their empire, they found an economic system based on groups of specialists. That the Inka moved these groups around and modified their organization and relative status is clear. They did not, however, originate the specialization system, but instead adapted it to their own use. Looked at in this light, the Chincha data provide support for the strategic flexibility of Inka statecraft in the face of the tremendous variability found within their Andean empire.

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NOTES

Chapter 2

[1] "Relation and declaration of the way in which this valley of Chincha and its neighbors were governed before there were Inkas and after they came until the christians [Spaniards] entered this land."

[2] "Notice of the way that there was in the government of the Indians in the time of the Inka and how the lands and tribute were distributed."

[3] For instance, the author of the "Aviso" writes that "of the thirty thousand men that were in this valley of Chincha, *today* there are only six hundred or a few more alive and all the lands that the dead possessed *have remained* vacant . . ." ("de los treinta mil hombres que avía en este balle de Chincha, no hay agora vivos sino seiscientos o poco más y todas las tierras que los muertos poseían han quedado vacas . . .") (Rostworowski 1970: 172, emphasis added). Referring to marriage rules, Castro and Ortega-Morejón state in the "Relación" that "this custom *is kept to this day* in all the valleys" ("y esta çirimonia se guarda el dia de [h]oy en todos los m[a]s val[l]es") (Crespo 1975:98, emphasis added).

[4] ". . . en lo cual la relación dellos que dello se puede dar es sólo por la que se ha tomado de indios viejos por personas que saben su lengua. . . ."

[5] ". . . ser ellos gente varia y sus relaciones en algunas cosas diferentes."

[6] "Los yungas no adoravan al sol sino a guacas."

[7] ". . . avía un solo mayor a quien obedecían y respetavan todos ellos, éste fue primero que Topa Inga Yupanqui."

[8] "Como los Ingas los señorearon, tornaron dellos muchas costumbres, y vsaron su trage, imitándoles en otras cosas que ellos mandauan, como vnicos señores que fueron."

[9] ". . . los naturales de Chincha no dexaron de adorar también en su antiguo templo de Chinchaycama."

[10] ". . . se hizieron grandes y sumptuosos aposentos para los reyes; y muchos depósitos . . . se hizo en este valle templo del sol."

[11] ". . . los Ingas no priuaron del señorío a los Caciques y principales."

[12] Murra (1980:163) defines the mitimaes as "colonists transported from one place to another for state purposes."

[13] The yanaconas were also known simply as "yana," and the mamaconas are usually referred to as "acllas." Murra (1980:163) defines these categories as men and women "removed from ethnic jurisdiction for state purposes." The difference between yana and aclla on the one hand and mitimaes on the other seems to be that the mitimaes were moved as community groups retaining an ethnic identity and rights and obligations in their place of origin, while the yana and aclla seem to have lost this identity.

[14] ". . . una yndia que estava en este valle de Chincha señalada pa[ra] el inga. . . ."

[15] ". . . el hermoso y grande valle de Chincha, tan nombrado en todo el Perú, como temido antiguamente por los más de los naturales . . . quando el marqués don Francisco Piçarro con sus treze compañeros descubrió la costa deste reyno, por todo ella le dezían, que fuesse a Chincha, que era la mayor y mejor de todo."

[16] "Este valle es vno de los mayores de todo el Perú: y es cosa hermosa de ver sus arboledas, y acequias y quantas fructas ay por todo él. . . ."

[17] "Llegado el Ynga [a] aquel valle, como tan grande y hermoso lo vio, se alegró mucho."

[18] ". . . por order del Hernando Pizarro, sacaron de las sepulturas de los Indios muertos que estavan junto al primer monasterio que el Padre Fray Domingo de Santo Tomás . . . fundó en el balle dicho . . . cien mil marcos de plata en vasijas grandes y pequeñas y otras [cosas] . . . todos en oro y plata. . . . Y después de ésto se ha sacado mucho oro y plata en aquel balle y hay mucho más por sacar. . . ."

[19] "El señorío de estos fue siempre seguro y próspero."

[20] ". . . avía en el valle de Chincha y en su jurisdicción treinta mil hombres tributarios."

[21] ". . . treinta caciques de dichos [tributarios], que cada uno tenía mil Indios a su cargo, y señores todos estos treinta."

[22] ". . . a ymitaçión del Cuzco dividió los yndios y puso señores desta manera que [h]obiese un curaca de mill yndios. . . ."

[23] ". . . que en todos los valles [h]uviese dos parçialidades una que se llamase hanan y otra lorin . . . ."

[24] In Quechua, "lurin" or "hurin" means lower and "hanan" means upper; these terms were frequently applied to the moieties in Andean communities in Inka times (*see* note 23; *also* Rowe, 1946:262–263).

[25] ". . . no entendían sino en sembrar maíz y otras semillas y raíces de que se sustentaban y mantenían."

[26] ". . . se ponía en depósitos y dello se llevava al Cusco e a Xavxa e a Pachacama o donde les mandavan. . . ."

[27] "Avía poblado por la costa de la mar diez mil pescadores, que cada día o los más de la semana entravan en la mar, cada uno con sus balsas y redes y salían y entraban en sus puertos

señalados y conocidos, sin tener competencia los unos con los otros, porque tenían en ésto como en lo demás, gran orden y concierto y amor y temor al Inga y a sus caçiques y éstos estaban poblados desde dos leguas antes de llegar a Chincha hasta es otra parte de *Lurinchincha* [sic], que hay de una parte a otra cinco leguas; y parecía la población de esta gente una hermosa y larga calle llena de hombres y mugeres, muchachos y niñas, todos contentos y gozosos por que no entrando en la mar, todo su cuidado era beber y baylar, y lo demás."

[28] ". . . mucha Chaquira de oro y muchas esmeraldas ricas y las vendían a los caçiques de Ica . . . ."

[29] ". . . entre ellos compraban y vendían con cobre lo que avían de comer y vestir . . . ."

[30] Many other authors have accepted Rostworowski's hypothesis of Chincha as a major pre-Inka trading power as fact (e.g., D'Altroy and Earle, 1985:195; Hosler, 1988:842; Shimada, 1991: LIV). Wallace (1991:258) notes the incongruities between the ethnohistoric and archaeological records but still accepts Chincha as a pre-Inka trading power.

[31] ". . . syn pasar a otra parte ni saber si no era por oydas que [h]avía m[á]s jente porque si pasava si no era en t[iem]po que [h]avía paz y treguas se matavan unos a otros . . ." Although it may reflect a Cuzco-centric view of pre-Inka barbarism, Castro and Ortega Morejón's statement concerning pre-Inka warfare among the south coast local polities is supported by Cieza's (1987 [1553]:205–206, Cap. LXIV) account of events on the south coast during the Spanish conquest of Peru; several Inka military leaders, along with Chachapoya and Cañari Indians, joined together with the people of Ica to attack Chincha. The Chinchas responded to this threat by sending messengers to the Spanish at Pachacamac to beg for aid; with five or six Spanish horsemen and several thousand Chincha Indians, the attack was held off and the people of Ica were brought under Spanish dominion.

[32] Even after the Spanish conquest, *Spondylus* was still actively traded on the north coast. Polo (1906 [1559]:227) wrote in the mid 16th century that Spaniards were doing very well trading "some seashells called Mollo . . . especially in Trujillo and its region" (". . . conchas de la mar que llaman Mollo . . . en especial en Trugillo y su comarca . . .").

[33] "oficios y cosas en que seruian al Ynga."

[34] ". . . los que eran oficiales pagasen el tributo en cosa de su oficio y no en otra. . . ."

[35] The *encomienda* was a Spanish grant of the rights to the labor of indigenous groups.

[36] ". . . entre estos labradores había algunos oficiales buenos plateros y el día de hoy han quedado algunos."

[37] Lizárraga's (1946 [ca. 1605]:90, Cap. XLVII) inclusion of this group among the "labradores" seems to argue against such an interpretation, but he also adjusts the numbers to make the total equal the requisite 30,000 tribute-payers. This account is rather late and may represent a post facto solution to an awkward discrepancy.

[38] ". . . partes conocidas y privadas donde pescan . . . ."

Chapter 3

[39] The "Aviso" says that the Chincha merchants bought food and other necessities with copper, but the document also differentiates the fishermen from the merchants. Thus, Model One does not specify the nature of the fishermen's local exchange.

Chapter 4

[40] Menzel's Chincha style is equivalent to Kroeber and Strong's (1924) Late Chincha I (Menzel, 1966; Menzel and Rowe, 1966: 64).

[41] See Chapters 7, 8, and 11 for a reconsideration of the chronological integrity of Menzel's late pre-Hispanic Chincha sequence.

[42] Uhle (1924:69) implied that the Inka destruction of the temple of Chinchaycamac is historical fact; unfortunately, there are no citations attached to Uhle's report. He may have been referring to the sources cited by Patterson (1985:164–165), who has written that the Pachacamac oracle told the Inka ruler Thupa Yupanki to build a house (branch oracle) for his son in Chincha, where he (Pachacamac) already had a "wife" (a related temple)—possibly the site of El Cumbe. Patteron's study suggests that the Inka would not have destroyed El Cumbe; the damage which Uhle observed probably resulted from the looting which began within a few years of the Spanish conquest (*see* Chapter 2).

Chapter 5

[43] After removing the artifacts, this column and a smaller one from Sector IV were sent to the Florida State Museum, where they await detailed analysis of the organic remains.

[44] This anomalous date falls at one of the ambiguous points on the Stuiver and Pearson (1986) calibration curve and could, in fact, represent a real age as old as A.D. 1400 or as young as A.D. 1680.

Chapter 6

[45] During the excavations at Lo Demás, the term "feature" was used as a catch-all designation to cover a wide variety of archaeological occurrences. In general, "features" were defined as anything that did not appear to be a primary deposition stratum. Thus, both construction elements such as walls and destruction elements such as pits or channels were labelled as features, as were lenses of limited areal distribution and some special finds such as intact guinea pigs or reed mats.

[46] Although filled with material from Complex D, this pit was cut into the floor that marks the top of Complex C and may more properly be assigned to that complex.

[47] According to Menzel (1976:243–245), based on her analysis of Late Ica pottery, Early Colonial Ica 10 was a time when the natives of the Ica valley used the interlude between the fall of the Inka empire and the consolidation of Spanish control to return to styles used before the Inka conquest of their valley. Among these revivals are imitation Chincha forms, recalling the immediately pre-Inka Ica 8 phase when Chincha had great influence in Ica.

[48] See Chapter 11 for a discussion of the use of the Inka *adobe* type in Building IV–2 and the probable elite status of the Sector IV inhabitants at Lo Demás.

Chapter 7

[49] Rims comprised 7.9% (279/3,552) of the sherd sample, but less than a third of all rims were preserved well enough to determine orientation and diameter. Decorated sherds are similarly few.

[50] As Rice (1987:210) points out, "All pottery has some function or utility," including elite or special purpose wares. As used by Menzel and in this study, utilitarian or domestic pottery is that for which the primary apparent use is as a tool, i.e., in one of Rice's (1987:208) "three broad realms [of domestic ceramic container use]: storage, transformation or processing, and transfer or transport."

[51] Although cooking is the most universal activity involving fire, any activity which requires placing a ceramic vessel on a fire would produce sooted sherds (Rice, 1987:235–236). An example would be metallurgy. However, the nonceramic remains from Lo

Demás provide no evidence for any activity involving fire except cooking (e.g., no slag from metallurgy), and food remains are the most abundant constituent of the excavated midden.

[52] Because of the small sample size and relatively nondiagnostic condition of most sherds, the following analysis is in terms of general shape categories rather than vessel types. Most of the shape categories from Lo Demás undoubtedly include more than one type and/or subtype, but a much larger sample must be acquired before these finer levels of classification can be defined.

[53] In the Lo Demás pottery assemblage, as well as in the Chincha pottery studied by Menzel (1966), oxidation or reduction firing seem to be deliberate choices related to decoration and shape. The reduced-fired sherds from Lo Demás are dark grey, generally thin and hard, often have incised or modeled decoration, and are usually highly polished.

[54] Marcus (1987*b*:28, Fig. 12) illustrates two sherds from Pingüino Buff wide-mouthed globular jars excavated at Cerro Azul, Cañete. Pingüino Buff is apparently a pre-Inka, Late Intermediate Period ware (Marcus 1987*b*:25). The exact form and orientation of the two rims cannot be determined from the figure provided by Marcus; the vessels appear generically similar to the Lo Demás angular rim bowls, but with a longer rim, somewhat like Menzel's (1966:85–86) "collared jars."

[55] However, Henrickson and McDonald (1983:632) state that "the maximum diameter [of serving/eating vessels] is . . . typically equivalent to the rim diameter, resulting in open, 'unrestricted' bowls."

[56] The assignment of many of the sherds to this category must be treated with caution because the sherds are broken above the corner point (where the neck meets the body; *see* Rice, 1987:218, Fig. 7.5). The illustrations show which neck sherds lack the corner point, and I have indicated in the text how many sherds assigned to each jar category include the corner point.

[57] I assigned these two sherds to the wide-mouthed jar category because they lack the corner point and could therefore have higher necks than do collared jars. The Huacarones probable collared bowl/jar sherds (Sandweiss, 1989:Fig. 29q–t) discussed above were assigned to the angular rim bowl category because they had the corner point, indicating that the neck was relatively short.

[58] With the exception of several miniatures, the height of bottles from the Uhle Chincha collections ranges from ca. 10 to 25 cm (Menzel, 1966:Appendix A).

[59] Because the height of the Lo Demás vessels cannot be reconstructed from the available sherds, it is possible that some of the sherds come from vessels which were short enough to be classified as dishes; thus, both bowls and dishes are potential analogues.

[60] Cuzco Inka pottery includes several shapes which might produce sherds somewhat similar to the angular rim bowls sherds from Lo Demás, especially Rowe's (1944:48, Fig. 8) Shapes F and J. However, the body form on these shapes is different from that of the most complete Lo Demás and Huacarones examples, and it is different from the published Cañete, Chincha, and Ica angular rim bowls.

[61] Because an analysis of the Huacarones ceramic assemblage is currently being carried out by Luís G. Lumbreras, I am awaiting his results before comparing Huacarones decoration with that on Lo Demás sherds.

[62] The dark brown observed on many sherds from Lo Demás may be a faded black; many of the designs seen in dark brown in Lo Demás are described by Menzel (1966) as black on vessels in the Uhle collection. Menzel's study used whole pots from graves, which might account for better color preservation.

[63] At the site of Hatunqolla near Lake Titicaca, Julien (1983:231) found that her three Inka-associated phases showed a transition from two to three lateral stems in the fern pattern. By Phase 3, only the three-strand stem was in use; based on Julien's analysis, Phase 3 would have begun around A.D. 1500, a date which is roughly consistent with other chronological indicators for Lo Demás. However, Julien's study is based on a small sample; there is no evidence to confirm or deny the areal extent of the trend which she noted, and the Lo Demás assemblage contains only one sherd with a fern pattern.

[64] Menzel (1966:Appendix B) assigns both of these vessels to her LIP 8/early LH Chincha Style. The fish on these pots most closely resemble an Ica 6 design (Menzel 1976:Plate 27–315).

[65] The post-Chincha pots have resin paint in the incisions, unlike the Lo Demás sherds. However, the different conditions of use and deposition could well explain the lack of paint on the latter examples.

Chapter 8

[66] Excavations in Sector I include Subunits A1, A2, A3, B3, C3, 1A–D, 2A–D, 3A–D, 4A–D, 10A, and 10D.

[67] The eyes are particularly important as chronological markers because the lenticular, grooved eye has its closest parallel in Inka figurines (Menzel, 1967:27).

[68] Menzel (1966:Appendix B) assigns the graves containing the decorated metal ear plugs to the Late Horizon and early Colonial Period. One of these graves (F–4) had a European glass bead, while the other two (including the one containing the ear plug with the closest similarity in design to the tweezers bird—Fig. 40) have only pre-Hispanic artifacts.

[69] Sr. Pachas told me that the rest of the collection, which he had given away to friends and relatives, consisted of the same kinds of metal pieces. However, I suspect that a larger number of finished or nearly finished artifacts may well have been part of the original collection; these are the kind of objects which would appeal to local collectors. Even so, the general conclusion that the pieces represent a set of materials from a workshop remains valid; the missing material would have helped define the kinds of artifacts produced by that workshop.

[70] Menzel (1976:40–42) found shallow dishes throughout the Late Intermediate Period and Late Horizon sequence in Ica; the Chincha specimen found by Vivanco most closely resembles the Phase 9 (Late Horizon, Inka occupation) versions from Ica.

[71] If the "Aviso" document is correct in stating that the fishing settlement ran for many kilometers along the shore to the north and south of "Chincha" (presumably La Centinela, *see* Chapter 2), then the bluff to the north of Lo Demás was part of the fishermen's territory. A metallurgical workshop located along or near the bluff would therefore be part of the fishing settlement.

[72] Some copper was also available in the Chincha area. Uhle (1924:91) reports an old copper mine at the petroglyph site of Huancor in the San Juan (Chincha river) valley, some 32 to 33 km inland from the coast. He indicates that the mine was worked in colonial times, but suggests that it may also have been used during the pre-Hispanic era. Uhle notes that the name of a nearby lateral quebrada, Yauritambo, "means 'copper harbor' in Quechua" (1924). I visited Huancor on several occasions in 1984, once with geographer/geologist Alan K. Craig. After inspecting the "mine" (a small hollow of only a few meters depth, width, and height) and the surrounding area, Dr. Craig concluded that the zone is one of contact metamorphism where mineralization of elements such as copper is probably widespread. He suggested that the copper deposits, though individually small, would be fairly numerous and of very high grade.

[73] Kroeber and Strong (1924:35) describe this type of wooden

object as "28 to 37 cm. long, with a round head or knob. The other end is sometimes sharpened to a point, but is always flattened."

[74] Minimum orifice diameter was measured from the interior of the sherd drawings at the most restricted surviving point. Often, the orientation of the sherd at the break indicated that the actual minimum diameter was less than that measured.

[75] Sectors I and IV each had one case of cobble cortex flake and wood fragment association. In Sector I, this association occurred in Stratigraphic Complex B (cat. 1732); the wood fragment had one clear cut mark. In Sector IV, the association occurred in level 26–4c of Subunit 26D (cat. 1725); the wood fragment did not show any clear cut marks, though it was charred. Neither of the cobble cortex flakes were among those analyzed by Kvietok for edge damage.

[76] The presence of a wool textile in Lo Demás raises the question of whether the wool (raw or as a finished textile) was imported, or whether it was obtained in situ from the camelids whose presence is documented in Sector IV (*see* Chapter 9). This issue is considered further in Chapters 11 and 12.

[77] Height is defined as the length of the central hole; width is the dimension perpendicular to this axis.

Chapter 9

[78] "MNI-indicators" vary according to class; this study uses the following criteria. For bivalves, we counted for left and right hinges and took the larger number as the MNI. For gastropods, we counted apices and/or fragments of the columellar axis comprising over 50% of the original height; the larger number equalled the MNI. *Fissurella* provided a special case: on this genus (keyhole limpets), the apex consists of an oval hole. Shell fragments with over 50% of this hole were considered as MNI-indicators. Chiton have eight plates; to calculate the MNI for this class, we divided the number of plates in a provenience by eight and rounded the result to the next highest integer. MNI was not counted for barnacles (*Balanus* spp.).

[79] *Spondylus* may briefly colonize the Peruvian coast as far south as Callao as a result of south-flowing, warm El Niño waters (Sandweiss, 1982:219). El Niño occurs at irregular intervals; strong events last about a year. However, although individual *Spondylus* larvae emplaced during such events might survive for several years and reach a noticeable size, they would be unable to reproduce after El Niño ended and the cool-water Humboldt (Peruvian) current returned; the resulting populations would be both limited in size and ephemeral in time. Under these circumstances, El Niño would not have provided a significant source of *Spondylus* shells for Peruvian rituals.

[80] According to a 17th century document cited by Rostworowski (1970:152), a piece of *Spondylus* "smaller than a fingernail"—like the Lo Demás specimens—had a high monetary value in the Colonial Period.

[81] Faunal, or zoogeographic, provinces are sections of coast containing a characteristic set of molluscan species. Olsson (1961:24) defines the Peruvian Province as running from "Punta Aguja at the southwestern end of Sechura Bay in northwestern Peru (lat. 5°40′S.) south to near Chiloe Island, Chile (near lat. 42°S.)." He further writes (Olsson, 1961:33) that "although the Peruvian Province extends well into the tropics and within a few degrees of the equator, its fauna is essentially one of cool or temperate waters, maintained partly by the Peruvian Current and by strong, inshore upwellings from depths."

[82] Molluscan species found at Lo Demás which may have been available on the Chincha coast during the past include *Mesodesma donacium, Protothaca thaca, Eurhomalea rufa, Thais haemastoma, Tegula atra, Crepipatella* spp., *Polinices uber,* and *Oliva peruvianus. Petricola denticulata* bores holes in colonial polychaete worm tubes. Because pieces of calcareous heads of polychaete worms are fairly common in Lo Demás (*see* Chapter 8, section on lithics), I suspect that the specimens of *Petricola* accompanied this material and were not acquired deliberately. The worm heads were probably collected on the Chincha shoreline.

[83] Cool water, indigenous Peruvian mollusk species which were probably imported to Lo Demás from other parts of the south coast include *Perumytilus purpuratus, Acmaea* spp., *Concholepas concholepas, Fissurella* spp., *Aulacomya ater, Argopecten purpuratus,* and *Choromytilus chorus.* All of these species except *Aulacomya ater* are very rare at Lo Demás, and even *A. ater* is not very common (*see* Table 27).

[84] The virtual absence of *Perumytilus purpuratus* combined with the importance of *Semimytilus algosus* in the Lo Demás molluscan assemblage strongly suggests that the Late Horizon Chincha shoreline had no rocks which extended into the upper intertidal zone. Wherever I have observed *Semimytilus* along the Peruvian coast, I have also seen *Perumytilus* whenever the rocks reached into the splash zone. In archaeological sites with access to upper and lower intertidal rocky zones, *Perumytilus* and *Semimytilus* tend to co-occur (e.g., El Paraíso, central coast—Sandweiss, 1985*b*).

[85] There are still some unsolved problems, however. As Koloseike (1969:150) pointed out, seasonal cycles and environmental conditions cause variations in meat weight that are not necessarily reflected in shell weight or linear dimensions. I know of no study that accounts for both of these factors, though Tomka (1980) does provide data for *Aulacomya ater* during several seasons. Appropriate experiments are possible, though time consuming; the principal result would probably be a larger (more realistic) error estimate for calculated meat weight values.

[86] In this context, I define "cultural preference" as any criterion by which people select certain items (mollusks) from the universe of those available. A partial list of such criteria includes palatability, ritual proscription, and differential access due to economic or social status.

[87] This dichotomy is not absolute. Environmental alterations or perturbations may result from human activity or from the synergistic effects of human and natural processes. A number of recent studies on shellfish communities on the Andean coast and elsewhere (e.g., Castilla and Duran, 1985; Hockey and Bosman, 1986) have shown that human predation has a significant effect on molluscan community composition. The effects of natural perturbations such as El Niño are even better known (e.g., Arntz, 1986; Arntz et al., 1985; Rollins et al., 1986). The crash of the Peruvian anchoveta (*Engraulis ringens*) stock in the early 1970s provides an example of probable interaction between human (overfishing) and natural (El Niño) processes (Cushing, 1981:218–219). The disappearance of *Choromytilus* from the Peruvian north coast following the Initial Period may be another such example.

[88] Changes in technology can affect availability; however, the technology involved in collecting mollusks is generally quite simple, and in sites occupied over relatively short periods (such as Lo Demás), technological innovation probably does not account for changes in species frequencies.

[89] Recognition of functional differences within a site (or between sites) depends on another set of interpretive assumptions.

[90] Grayson (1984) demonstrates the potentially misleading effects of different levels of aggregation of faunal remains on the calculation of MNI. The more excavation units that are aggregated before calculating MNI, the smaller the MNI. Grayson suggests that a partial solution to this problem is to use NISP. However, most of the problems that Grayson identifies relate to vertebrates; mollusks have so few diagnostic skeletal elements (one or two) that aggregation effects are minimal. To control for any possible problems, however, I checked the relationship between *Donax* and *Semimytilus* using MNI calculated from each provenience within each complex and using MNI calculated from the remains aggregated by complex. I found no significant difference. Furthermore, the reversal in these species is equally real in terms of MNI, NISP, and shell weight.

[91] In the sampled subunits, *Semimytilus* was more abundant than *Donax* by weight in 52 of 60 proveniences in Complex D, while *Donax* was more abundant in 102 of 125 proveniences in Complexes A to C.

[92] These taxa are *Choromytilus chorus, Aulacomya ater, Perumytilus purpuratus, Spondylus* spp., *Argopecten purpuratus, Fissurella* spp., *Acmaea* spp., *Calyptraea trochiformis, Concholepas concholepas,* and *Chiton* spp.

[93] However, the one *worked* piece of *Spondylus* came from Sector IV (*see* Chapter 8, section on Bone and Shell Objects).

[94] Mariano did not separate skeletal elements by left and right, so MNI estimates based on paired elements were calculated by dividing the total number of each paired element by two and rounding up to the nearest integer. The resulting MNI estimates are thus conservative.

[95] The genera for which Mariano could not make species identifications all have specific representatives which are indigenous to the Humboldt Current.

[96] Industrial, refers here to acquiring fish as a commodity for exchange or payment of tribute, not simply for local subsistence.

[97] To determine the validity of this observation, further research will have to: 1) quantify the amount of salt precipitating from the various bones, and 2) measure the amount of salt present on modern bone specimens from fresh and salted fish and from terrestrial animals.

[98] However, the relative lack of vertebrae must result to some degree from the use of ¼″ screen. Although definitive statements of the ratio of cranial to postcranial elements in the site must await the planned analysis of unscreened column samples by Elizabeth S. Wing and Elizabeth J. Reitz (1987), my impression from watching the screen during excavation is that cranial elements will prove to be truly overabundant relative to postcranial ones.

[99] The four Clupeiformes taxa found at Lo Demás have average sizes ranging from about 15 to 25 cm in length (Mariano, 1984).

[100] The Perciformes taxa found at Lo Demás range in average size from 30 to 35 cm to over 60 cm in length (Mariano, 1984).

[101] MNI parallels NISP fairly closely, though with a consistently lower proportion of sardines.

[102] The two bones tentatively identified as turtle, the 37 amphibian bones (*Batrachophrynus* sp. and unidentified frog/toad), and the four bones tentatively identified as lizard are included in this section.

[103] "El sacrificio ordinario es de cuyes, de los cuales se sirven mal, no sólo para sacrificios, sino para adivinar por ellos y para curar con ellos. . . . Cuando los han de sacrificar, unas veces los abren por medio con la uña del dedo pulgar. . . ."

[104] These statistics include only the disarticulated bones; they do not include the intact guinea pigs, which were not found in the sampled subunits, nor the grey-headed albatross (*Diomedea chrysostoma*) from the 1983 excavation.

[105] The piece of possible cow hide, a 1.5 cm square, is the only artifact from the excavations at Lo Demás which appears to be of European origin (one unmodified plant specimen, also from Complex D, is from an Old World plant). The cowhide may be intrusive, or its location near the surface in Complex D may indicate that Lo Demás was abandoned shortly after the Spanish conquest (*see* Chapter 11).

[106] Unidentified bones accounted for 8.0% of the sample in Sector I versus 28.5% in Sector IV (*see* Table 47). Percentages of rodents (domestic and wild) calculated on the total sample for each sector (i.e., including unidentified bones) are much more similar than the results cited in the text and in Table 48, which were calculated on the sector samples minus the unidentified bones; rodents comprised 27.1% of the total Sector I sample versus 33.0% of the total Sector IV sample. Using the total samples does not seriously affect the other results; birds remain twice as common in Sector I (56.3% versus 23.1%), large terrestrial mammals are three and a half times as frequent in Sector IV (8.3% versus 2.4%), and sea mammals are still similar (4.2% in Sector I and 3.1% in Sector IV).

[107] The majority of the "unknown" specimens could not be identified because of flattening or other damage to the feces.

[108] However, see Chapter 10 for evidence indicating that gourd utensil manufacture and possibly fiber processing took place in Sector IV and may also have provided goods for tribute and/or exchange.

Chapter 10

[109] This figure does not include 224 specimens identified from Stratigraphic Complex A in Sector I, which are not considered in the following analyses because of the scarcity of remains and because of the ephemeral nature and uncertain affiliation of this complex (*see* Chapter 5).

[110] My primary source for medicinal uses of plant species is Morton (1981), which is primarily concerned with Middle America. No comparably detailed source exists for the Andean region, although there are a number of local studies and a review of ethnohistoric and historic evidence for indigenous plant use by Chavez Velazquez (1977). However, about half of the species found in Morton and listed in Table 52 as having potential medicinal uses are mentioned by Towle (1961). Furthermore, many of the species listed by Morton (1981) have active ingredients whose properties would likely have been recognized by ancient Peruvians.

[111] Although the number of identified specimens—10,345 for Sector IV, 12,247 for Sector I— is not very different, the surface area and volume of the analyzed deposits does vary significantly between the two areas. In Sector IV, only 1 m^2 and ca. 1.25 m^3 were analyzed, while the totals for the Sector I plant sample are 6 m^2 and ca. 4.00 m^3. Thus, the density of plant remains by NISP is almost three times as great in the Sector IV sample as in that from Sector I. The samples from the two areas were deposited over approximately the same span of time (*see* Chapter 11).

[112] This figure differs from that reported in Sandweiss (1989) due to the addition of 16 coca (*Erythroxylum* sp.) fruits identified

after 1989 in the unidentified portion of the Lo Demás botanical sample (A. Cano E., personal communication, 1990).

Chapter 11

[113] Kroeber and Strong (1924) do not use the terms "Chincha style" or "Late Horizon"; Menzel (1966) applies these labels to what Kroeber and Strong (1924) called Late Chincha I and Late Chincha II/Inka with a few minor adjustments.

[114] L. Lumbreras is currently analyzing the pottery excavated at Huacarones; he believes that the lower levels from this site contain an early Chincha pottery style (C. Morris, personal communication, 1985). Lumbreras's study should provide important information relative to the origins of Menzel's (1966) Chincha style. As the Lo Demás study shows, surface collections and grave lots are not always reliable sources of information for distinguishing short-term chronological change.

[115] Many of the fish remains in Sector I—particularly the abundant cranial elements—represent debris from fish processing, but the presence of vertebrae suggests that fish were also consumed there.

[116] Not all of the guinea pigs raised at the site or brought there were eaten: some were used in curing rituals (*see below*, section on *Curanderos*).

[117] Although this sherd might have come from a provincial vessel made under Inka supervision, rather than from a plate made in Cuzco, it still indicates a closer contact with the Inka administrators and the Inka redistributive network than would a local imitation.

[118] Sector IV was not, however, the seat of the paramount lord of Chincha, which would have been La Centinela (Fig. 1, PV 57–1) or possibly the nearby Huaca de Tambo de Mora (Fig. 1, PV 57–2) as Uhle (1924:64–66) suggested.

Chapter 12

[119] The "Aviso" (Rostworowski, 1970:170) states that each 1,000 tribute payers in Chincha had a lord ("cacique"). Although the actual sizes of groups need not have been exactly (or even nearly) 1,000, the fact that the "Aviso" ("Aviso," Rostworowski, 1970:170–171) numbers the three major specialized groups (fishermen, laborers/farmers, and merchants) in multiples of 1,000 suggests that lords rather than tribute-payers were censused. If this is the case, then there were ten local-level fishing lords (Chapter 2; *see also* Netherly, 1977 for an extended treatment of local-level lords on the north coast).

[120] Moseley and Mackey (1972:77) do not actually name the site they discuss, but Kautz and Keatinge (1977:95) determined that Medaños La Joyada is the only site to which Moseley and Mackey could have been referring.

GLOSSARY

Aclla (also **mamaconas**). Chosen women removed from their communities and placed in Inka state installations to produce special items, such as fine textiles, on a permanent basis. *See* Note 13.

Adobe. Sun-dried mud brick.

Anchovetera. Small mesh net appropriate for taking *anchoveta* (*Engraulis ringens*).

Atawalpa (also **Atahuallpa**). Inka ruler for a brief period in 1532; son of Wayna Qhapaq and brother of Wascar, whom he defeated and captured in 1532 just prior to the arrival of the Spaniards under Pizarro. Atawalpa was captured by Pizarro in Cajamarca (north Peru) and was executed in 1533.

Ayllu. Basic Andean social unit.

Caballito. A Spanish word meaning literally "little horse"; refers to a single person fishing raft of bundled reeds used by traditional Andean fishermen.

Caçique. Lord or chief.

Caçique principal. Paramount lord.

Camelid. A member of the camel family; in the Andes, there are two wild (vicuña and guanaco) and two domesticated (llama and alpaca) camelids.

Cañete. The next valley north of Chincha. The dry Quebrada de Topará lies between Chincha and Cañete.

Cervid. A member of the deer family. Several wild cervids are found in the Andes.

Chimu. An empire that arose in the Moche valley of the Peruvian north coast as a local polity in the Middle Horizon and began territorial expansion in the Late Intermediate Period (beginning ca. A.D. 1100); the Chimú conquered most of the coast from Lima to Tumbes and were conquered in turn by the Inka around A.D. 1470.

Cuadrado. A Peruvian measurement of net mesh size equivalent to the length of one side of the mesh.

Curandero. A Spanish term for a healer or folk doctor; *curanderos* in the Andes are often ritual specialists.

Dedo. A rough Peruvian net mesh size measurement referring to the number of fingers which can fit in one mesh.

Early Horizon (abbr. **EH**). A period of increased interregional interaction associated in part with the spread of Chavín religion, dating between about 900 and 200 B.C.

Early Intermediate Period (abbr. **EIP**). A period following the Early Horizon and characterized by strong regional identities and the florescence of many art styles, dating between about 200 B.C. and A.D. 600.

El Niño. A recurrent environmental perturbation characterized by a south-flowing warm coastal current displacing the normal, north-flowing Humboldt Current. The increased water temperature disrupts the normally teeming marine life and brings torrential rains to the desert coast of Peru, causing flooding. The negative effects of El Niño follow a marked latitudinal gradient from north to south, grading into areas which actually benefit from El Niño.

Encomienda. A grant of rights to the labor of indigenous groups made by the Spanish government to individuals called *encomenderos* during the first half century of Spanish rule in the Andes.

Estirado (also **plana**). A Peruvian net mesh size measurement made by pulling the mesh from opposite corners and measuring the maximum extension; equal to twice the *cuadrado* measurement.

Humboldt Current (also **Peru Current**). The normal, north-flowing, cold-water coastal current off Peru, responsible for the coastal desert and the rich marine life of the region.

Huaca. A Quechua term originally referring to a shrine or sacred object, as in the early colonial documents. Now generally used to refer to a pre-Hispanic site, esp. a mound or pyramid.

Ica. A major valley system to the south and east of the Paracas peninsula; home to a Late Intermediate Period culture closely linked to Chincha.

Inka. Refers to the empire which expanded from Cuzco in the southern highlands of Peru and conquered most of the Andean region from northern Ecuador to northwest Argentina and Chile, between about A.D. 1440 and the Spanish conquest in A.D. 1532. This term also refers to the paramount ruler of the empire ("the Inka") and to the Cuzco-area culture which gave rise to the empire.

Labrador (pl. **labradores**). A Spanish term meaning "laborer"; in early colonial documents, often (but not exclusively) refers to farmers.

Late Horizon (abbr. **LH**). The period of the Inka empire (ca. A.D. 1440–1532); in a given area, the Late Horizon begins with the arrival of Inka influence. The Late Horizon follows the Late Intermediate Period and is the final pre-Hispanic period of the central Andes.

Late Intermediate Period (abbr. **LIP**). A period characterized by strong regional states, dating ca. A.D. 1100 to 1440 (slightly later in areas conquered later by the Inka). The LIP ends with the Inka conquest.

Llanke. A Quechua term referring to a sandal type used in pre-Hispanic Peru; made of cotton or vegetal fiber cord with straps of the same material or of polychrome wool.

Lomas. Seasonally fog-covered coastal hills; often used to refer to the xerophytic (fog-based) vegetation which flourishes during the winter on these hills.

Mallero. Spanish for "net-gauge," a tool used to make and repair nets.

Mamacona. See **aclla**.

Mayordomo. A Spanish term used in early colonial documents to refer to an Inka administrator placed over conquered groups.

Mercader (pl. **mercaderes**). A Spanish term meaning "merchant"; there is some debate as to whether its use in early colonial documents really refers to entrepreneurial merchants or some other category of exchange specialists.

Meseta. Tableland.

Middle Horizon (abbr. **MH**). A period of increased regional interaction between the Early and Late Intermediate Periods, dating ca. A.D. 600 to 1100. The Middle Horizon is the time of the Huari empire.

Minimum Number of Individuals (abbr. **MNI**). The largest number of individual animals definitely represented by a given faunal assemblage; may be less than the actual number of individuals originally deposited (hence *minimum* number).

Mitimaes (also **mitmaq**). Groups of people permanently resettled from one part of the empire to another by the Inka to carry out economic (sometimes specialized) and other functions. Mitimaes retained their ethnic identity, as well as rights and obligations in their community of origin. *See* notes 12 and 13.

Mitmaq. See **mitimaes**.

Mullu. A Quechua term referring to the *Spondylus* bivalve mollusk native to the warm waters of Ecuador. *Spondylus* was extremely important in central Andean ritual, and it was traded south to Peru beginning in the Late Preceramic Period. By the latest pre-Hispanic periods (after ca. A.D. 1000), it appears in great quantities in central Andean sites.

Number of Identified Specimens (abbr. **NISP**). The total count of identified plant or animal specimens in a given assemblage.

Oficial (pl. **oficiales**). A Spanish term used in early colonial documents to refer to artesans and other specialists.

Operculum (pl. **opercula**). A disk used by snails to seal off the entrance to the shell; often found separate from the shell, as it is articulared only by soft tissue.

Pachacamac. The largest and most important religious pilgrimage center on the Peruvian coast, located in the Lurín valley just south of Lima. Pachacamac submitted to the Inka by treaty rather than conquest, and the site maintained its prestige and power through the Late Horizon.

Pachakuti (also **Pachacutec**). Inka ruler from ca. 1438–1463 (Rowe, 1946:203). Began the expansion of the empire from Cuzco; sent the first expedition to Chincha under Qhapaq Yupanki.

Parcialidad (pl. **parcialidades**). A Spanish term used in early colonial documents to refer to native social units of different dimensions. On the coast, at least, *parcialidades* were paired asymmetrically to form successively larger units. *Parcialidades* could be composed entirely of specialists.

Pejerreyera. Small mesh net appropriate for taking pejerrey (*Odontesthes regia regia*).

Peru Current. See **Humboldt Current**.

Pescador (pl. **pescadores**). A Spanish term meaning "fisherman." In early colonial documents for the Peruvian north coast, it can also refer to a language or dialect spoken by the native fishermen.

Pisco. The next valley south of Chincha; also the colonial and modern port at the mouth of that valley.

Plana. See *estirado*.

Platero. A Spanish term meaning "silversmith."

Qhapaq Yupanki (also **Capac Yupanqui**). Inka general in the middle 1400s, sent by the emperor Pachakuti to conquer Chincha.

Quechua. The native language of the Inkas, spread by them throughout much of the Andes.

Quincha. Cane and mud (wattle and daub) used to make walls.

Quipu. Knotted strings used by the Inka as mnemonic devices to record accounts, both narrative and numerical.

Repartimiento. A Spanish term referring to Spanish administrative units roughly parallelling preconquest polities within the Inka empire.

Serrano. A Spanish term referring to a person from the *sierra*, or highlands.

Tapia. Puddled mud and/or rammed earth, used for walls.

Thupa 'Inka Yupanki (also **Topa Inca Yupanqui**). Inka ruler, son of Pachakutec. Ruled with his father from ca. 1463–1471, on his own from ca. 1471–1493 (Rowe, 1946:203). Continued the expansion of the empire; consolidated Inka control over Chincha.

Topará. A dry quebada (canyon) just north of the Chincha valley, between Chincha and Cañete. Also the name of a cultural tradition centered in the coastal area from Cañete to Pisco (including Chincha) and dating to the late Early Horizon and early Early Intermediate Period.

Tupu. A Quechua term meaning a cloak pin used to fasten women's mantles.

Visita. A Spanish term used in early colonial documents to refer to official inspections carried out by officials of the Spanish colonial administration. Each *visita* generally had a standard questionnaire, and each informant's answers were translated if necessary and recorded by a scribe.

Wascar (also **Huascar**). Inka ruler from 1527–1532, son of Wayna Qhapaq. Embroiled in civil war with his brother Atawalpa, he had been defeated and captured just prior to the arrival of the Spanish Conquistadores in 1532.

Wayna Qhapaq (also **Huayna Capac**). Inka ruler from ca. 1493–1527 (Rowe, 1946:203), son of Thupa Yupanki.

Yanacona (also **yana**). Men removed from their communities and placed in Inka state installations to carry out special activities on a permanent basis. *See* note 13.

Yunga. A Quechua term referring to the coastal zone, also used to refer to coastal peoples and languages.

Zapatero. A Spanish term meaning "shoemaker."

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